THE QUARTERLY REVIEW *of* BIOLOGY

VOLUME 17

1942

Published by

THE WILLIAMS & WILKINS COMPANY

BALTIMORE

U. S. A.

BOSTON UNIVERSITY
COLLEGE OF LIBERAL ARTS
LIBRARY

Chester C. Corbin Library Fund
Bound June, 1943

THE QUARTERLY REVIEW OF BIOLOGY

FOUNDED BY RAYMOND PEARL

B. H. WILLIER, *Editor*
The Johns Hopkins University

ASSISTED BY

R. W. HEGNER
Contributing Editor
The Johns Hopkins University

MAUD DEWITT PEARL
Assistant Editor
The Johns Hopkins University

ADVISORY BOARD

ANATOMY	LEWIS H. WEED	*The Johns Hopkins University*
ANTHROPOLOGY	A. L. KROEBER	*University of California*
BEHAVIOR AND COMPARATIVE PSYCHOLOGY	K. S. LASHLEY	*Harvard University*
BOTANY	IRVING W. BAILEY	*Harvard University*
CYTOLOGY	CHARLES W. METZ	*University of Pennsylvania*
ECOLOGY	THOMAS PARK	*University of Chicago*
EMBRYOLOGY	E. G. CONKLIN	*Princeton University*
EXPERIMENTAL MORPHOLOGY	ROSS G. HARRISON	*Yale University*
GENERAL PHYSIOLOGY	LAWRENCE J. HENDERSON	*Harvard University*
	G. H. PARKER	*Harvard University*
GENETICS	R. A. EMERSON	*Cornell University*
	T. H. MORGAN	*California Institute of Technology*
GEOGRAPHICAL DISTRIBUTION AND TAXONOMY	ALEXANDER G. RUTHVEN	*University of Michigan*
PALEONTOLOGY	JOHN C. MERRIAM	*Carnegie Institution*
ZOOLOGY	FRANK R. LILLIE	*University of Chicago*

QH
301
E261
v. 17

22

CONTENTS

No. 1, March, 1942

PAGE

A Re-examination of Thoreau's "Walden" ..... *Edward S. Deevey, Jr.* 1
Control of Swimming Position by Mechanical Factors and Proprioception ..... *John H. Lochhead* 12
The Pituitary Body in Giant Animals, Fossil and Living: A Survey and a Suggestion ..... *Tilly Edinger* 31
Structural Relations in Cell Respiration ..... *Barry Commoner* 46
Supernumerary Mammae, with Special Reference to the Rhesus Monkey ..... *Harold Speert* 59
New Biological Books:
Biography of a Statesman ..... *William Travis Howard* 69
Brief Notices 72

No. 2, June, 1942

The Relation of Adaptability to Adaptation ..... *G. F. Gause* 99
The Phylogeny of Social Nesting Habits in the Crotophaginae ..... *David E. Davis* 115
The Innervation of the Adrenal Gland ..... *Harry A. Teitelbaum* 135
The Integration of Vegetation ..... *W. F. Gericke* 149
New Biological Books:
Brief Notices 163

No. 3, September, 1942

Developmental Processes and Energetics ..... *Albert Tyler* 197
Contributions to the Physiology of Form Generation in the Development of the Sea Urchin ..... *Per Eric Lindahl* 213
Rudimentary Digits in Primates ..... *William L. Straus, Jr.* 228
On the Interpretation of Radiation Experiments in Genetics ..... *U. Fano* 244
New Biological Books:
Increase and Multiply ..... *Antonio Ciocco* 253
Brief Notices 254

No. 4, December, 1942

The New Perspective in the Halophytes ..... *V. J. Chapman* 291
The Determination of the Castes of Social Insects ..... *S. F. Light* 312
Chemistry of "Eye Color Hormones" of *Drosophila* ..... *Boris Ephrussi* 327
Developmental Processes and Energetics (*Concluded*) ..... *Albert Tyler* 339
New Biological Books:
Nati Sunt Mures, et Facta Est Confusio ..... *G. Evelyn Hutchinson* 354
Brief Notices 357
Index 390

VOL. 17, NO. 1 March, 1942

THE QUARTERLY REVIEW
of BIOLOGY

A RE-EXAMINATION OF THOREAU'S "WALDEN"

BY EDWARD S. DEEVEY, JR.

Osborn Zoological Laboratory, Yale University; and Department of Biology, The Rice Institute

INTRODUCTION

WHEN we regard Thoreau simply as an observer or as a natural historian," says Burroughs (1), "there have been better, though few so industrious and persistent. He was up and out at all hours of the day and night, and yet he saw and recorded nothing new. It is quite remarkable.... He has added no new line or touch to the portrait of bird or beast that I can recall.... He had not the detective eye of the great naturalist.... To the last, his ornithology was not quite sure, not quite trustworthy."

In this paper I propose to show that, however untrustworthy Thoreau's ornithology may have been, his contribution to at least one natural science, limnology, was original and genuine.

The bulk of Thoreau's limnological observations are set down in *Walden*, although some very important material is confined to his *Journal* and remained unpublished until long after his death. These notes, like his other records of natural history, are fragmentary and discursive, conforming to no methodical program of study or presentation. Nevertheless they have a great intrinsic interest for the ecological reader, and a renewed acquaintance with *Walden* prompted a journey to that lake, the results of which are described below.

The field observations were made on August 6, 1939, during a brief holiday from the Biological Survey of Connecticut lakes then being conducted by the Connecticut State Board of Fisheries and Game. The technical and analytical methods used are referred to elsewhere (2). I am deeply indebted to Professor G. E. Hutchinson for invaluable advice and encouragement, for investigating the history of the discovery of thermal stratification, and for the collection of a water sample from Walden Pond on July 16, 1939. My wife, Georgiana Baxter Deevey, rendered indispensable assistance in the field and in the laboratory. Facilities and equipment were generously provided by the Osborn Zoological Laboratory, and acknowledgment is made to the officials of the Rice Institute Library and the Mirabeau B. Lamar Library of the University of Texas for many courtesies. The manuscript has been read by Dr. A. D. McKillop, of The Rice Institute, and by Dr. Henry Seidel Canby, editor of *The Saturday Review of Literature*.

LIMNOLOGY OF WALDEN POND

Location and hydrography

The lake on whose banks Thoreau spent two of the most profitable years of his life (from July 4, 1845 to September 6, 1847) is in the town of Concord, Massachusetts, where he was born. The physiography of the Concord region bears witness to the activity of the Pleistocene ice sheets, as may be seen by inspection of the U. S. Geological Survey topographic map (Framingham quadrangle). Fig. 1, based on part of this map, shows the disorganized stream pattern and abundant undrained depressions so characteristic of a glaci-

BOSTON UNIVERSITY
COLLEGE OF LIBERAL ARTS
LIBRARY

ated landscape. Walden Pond, a seepage lake, is situated at an elevation of about 140 feet. The fact that the lake fills the bottom of a closed basin whose walls rise steeply nearly forty feet above the shore line suggests that the concavity is of kettle origin; this hypothesis is supported by the morphometry of the lake, but time did not permit the making of any geomorphic studies.

visit, it was essential to make another. The procedure adopted was the one used in limnological surveys of Connecticut lakes (2); an aerial photograph was obtained from the Fairchild Aerial Surveys, Incorporated, and the outline traced. Lines were chosen between conspicuous points on the lake shore, and soundings made at intervals of ten oar strokes, using a lead weight lowered from a

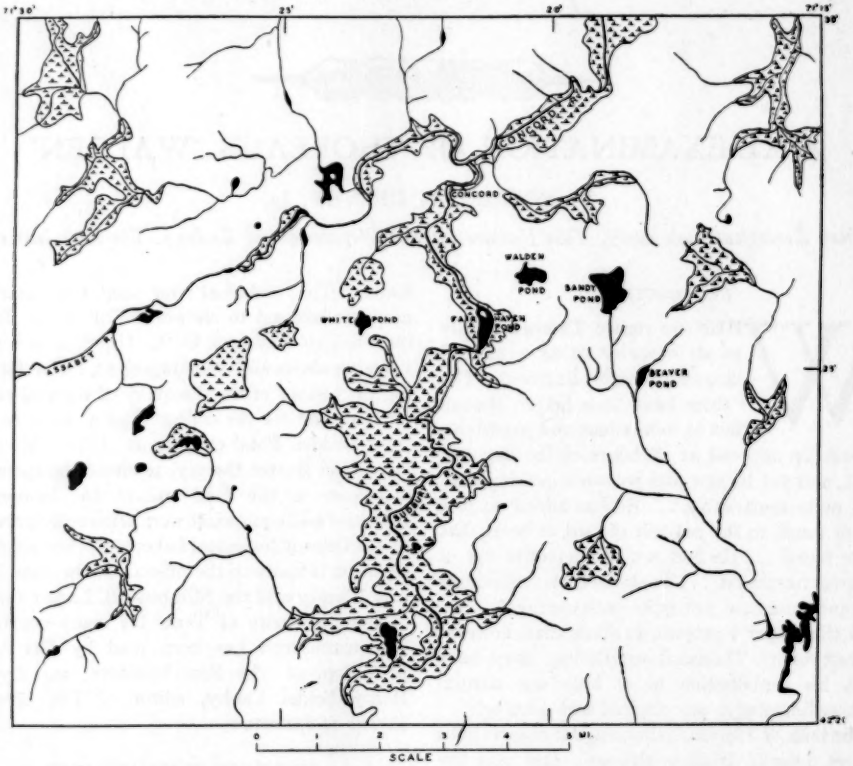


FIG. 1. SKETCH MAP OF THOREAU'S "LAKE DISTRICT," BASED ON U. S. GEOLOGICAL SURVEY TOPOGRAPHIC MAP (FRAMINGHAM QUADRANGLE)

Because he was amused by the local legend that Walden Pond is of infinite depth, and to satisfy his highly individual curiosity about the lake, Thoreau was at pains to sound it "with compass and chain," in the winter of 1846, and plotted his results on an outline map. This map, which is reproduced in Fig. 2 by courtesy of the Huntington Library, was published in the first edition of *Walden* but was withdrawn from later issues. As this map was inaccessible at the time of my

hand winch on music wire. The lake is small and well protected from wind, and so this method may be expected to give unusually reliable results. The map is shown in Fig. 3.

The similarity between the two maps is in some respects so close as to be startling (provided it is realized that, by modern convention, Thoreau's map is "upside down"). It is certain that the outline map used by Thoreau was his own, for a county map published by H. F. Walling in 1852

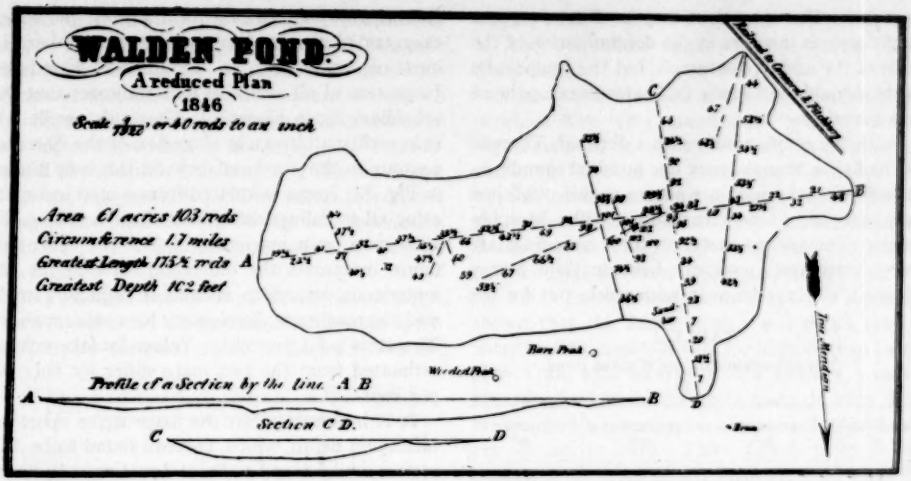


FIG. 2. THOREAU'S MAP OF WALDEN POND, REPRODUCED FROM THE FIRST EDITION OF "WALDEN" BY COURTESY OF THE HUNTINGTON LIBRARY, SAN MARINO, CALIFORNIA
Notice that by modern convention the map is "upside down."

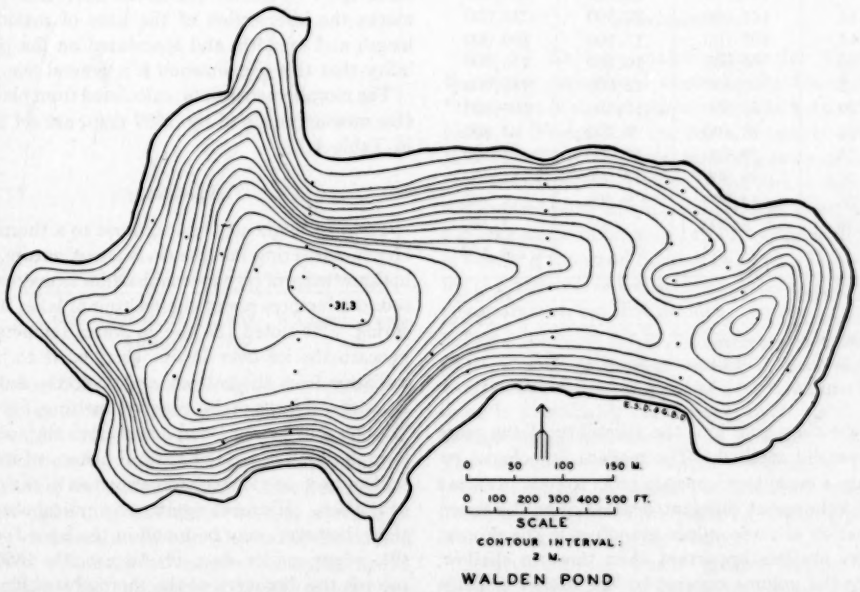


FIG. 3. BATHYMETRIC MAP OF WALDEN POND, FROM DATA OBTAINED AUGUST 6, 1939

gives credit for the outlines of Walden and White Ponds to "H. D. Thoreau, Civil Engineer" (3). The aerial survey map is almost precisely congruent with Thoreau's; moreover, the area of the lake as given by him, 24.98 hectares, is remarkably close to that computed from my map, 24.82

hectares. The agreement may be deceptive, as a slight error is inherent in the determination of the scale of the aerial photograph, but the comparison offers valuable testimony to Thoreau's competence as a surveyor.

With the entire winter at his disposal, Thoreau (4) had time to make over one hundred soundings, seventy-five of which are shown on his published map; only forty-nine were made in 1939. Morphometric comparisons based on these soundings are very instructive, not only because they betray Thoreau's inexperience in such work, but for the insight they give into the reliability of the more convenient method. The modern limnologist requires a bathymetric map in order to compute areas and volumes at different depths. For the determination of these values soundings in the deepest water are less important than those in shallow, since the volume covered by the deeper isobaths is small. In emphasizing the depths of the lake basin Thoreau neglected the shallows, which can be defined with greater confidence from the later map; when he said (5) "there is a bar across the entrance of our every cove, or particular inclination; each is our harbour for a season," he either exaggerated the probable extent of the bars in question or referred to unpublished soundings. Inspection of all available data indicates that the subsidiary basin shown by Thoreau's profile AB is in reality an irregular extension of the 20-meter contour to the southeast beyond the form shown in Fig. 3. Areas calculated from a map incorporating all soundings differ from those based on the 1939 map by a maximum of 29.6 per cent; this figure represents the difference between the 30-meter contours, which are almost negligibly small, and the maximum discrepancy for contours above 28 meters is 8.1 per cent. Values for lake volume estimated from the two maps differ by only 0.6 per cent.

TABLE 1

Morphometric data for Walden Pond
1939

CONTOUR m	AREA WITHIN m^2	AREA BETWEEN m^2	VOLUME m^3
0	248,200	25,600	470,600
2	222,600	21,900	423,200
4	200,700	20,100	381,100
6	180,600	19,300	341,500
8	161,300	16,600	305,800
10	144,700	20,100	269,100
12	124,600	20,900	228,000
14	103,700	17,100	190,000
16	86,600	16,100	156,900
18	70,500	12,000	128,900
20	58,500	10,100	106,800
22	48,400	9,200	87,500
24	39,200	10,300	74,500
26	28,900	15,000	41,900
28	13,900	9,800	17,100
30	4,100		1,250
			3,224,150

Mean depth..... 13.0 m.
Perimeter..... 2,535 m.
Shoreline development..... 1.75
50 per cent of volume covered by 6-m. contour.

It is interesting that the maps agree upon the maximum depth, which Thoreau found to be 31.1 meters, and I found to be 31.3 meters. As variations of the lake level amounting to two meters or more are known to occur (6), this approximation may be put down in part to coincidence, but the two soundings were made at almost exactly the same spot. Thoreau (7) noted that this point marks the intersection of the lines of maximum length and breadth, and speculated on the possibility that this phenomenon is a general one.

The morphometric data, calculated from planimeter measurements of the 1939 map, are set forth in Table 1.

Temperatures

Thoreau frequently had recourse to a thermometer in answering his questions about nature, and his knowledge of physics enabled him to make some sound inferences about the melting of lakes in the spring. He noted the rise in water temperature beneath the ice over shoals, ascribed it to back-radiation from the bottom, and correctly deduced that the difference in time of melting between Walden and Sandy Pond arises from their difference in depth (8). The natural history of ice has seldom been so glowingly described as in the pages of *Walden*. His most significant physical observations, however, may be found in the later *Journal* (9), where under date of August 22, 1860, he records the discovery of the thermal stratification of Walden Pond. The method employed was crude; he filled a bottle with water from the surface, stoppered it, and after lowering it to the bottom, allowed half an hour for the establishment of thermal equilibrium. The temperature was re-

corded after raising the bottle. Unfortunately only two determinations, at 50 and 100 feet, were thus made, and on the mistaken but natural assumption that the fall in temperature with depth was linear he calculated the average decrease to be one degree Fahrenheit in five feet (10). The biological importance of his discovery did not escape Thoreau, who remarks, "How much this varied temperature must have to do with the distribution of fishes in it! The few trout must oftenest go down below in summer."

Because of its unusual depth and sheltered situation Walden Pond has an exceptionally cold hypolimnion; the temperature at 30 meters in August,

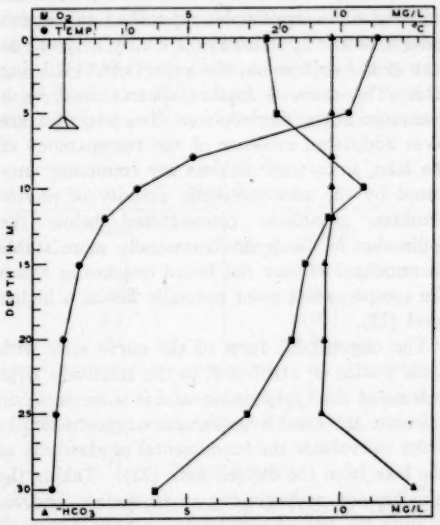


FIG. 4. LIMNOLOGICAL DATA FOR WALDEN POND, AUGUST 6, 1939

1939, was 5.26 degrees Centigrade, as measured with a reversing thermometer. In other respects the temperature curve shown in Fig. 4 is normal. Walden, however, acquires a surprising amount of heat during the summer season. The annual heat budget can not be calculated without a series of winter temperatures, but the wind-distributed heat, or summer heat income (assuming homothermy at 4°C.) amounts to 17,300 calories per square centimeter of lake surface. This value is considerably in excess of any observed in Connecticut lakes; Wononscopomuc Lake, which closely resembles Walden in depth, has a summer heat income of only 10,800 cal. per sq. cm., and the largest value observed was 12,800 cal. per sq. cm. in the somewhat shallower but larger East Twin Lake.

None of these lakes is of the first thermal class, in which Birge (11) placed lakes "whose size and depth are such as to permit [them] to acquire the maximum amount of heat possible under the weather conditions of the season." Such lakes in the eastern United States have summer heat incomes of at least 24,000 cal. per sq. cm.. and annual heat budgets between 30,000 and 40,000 cal. per sq. cm. Tressler and Bere (12) have recently shown that the limits of area and depth set by Birge for first-class lakes are too high; Sylvan Lake, New York, with an area of 50.6 hectares, a maximum depth of 38 meters, and a mean depth of 21.6 meters, had a summer heat income of 24,000 cal. per sq. cm. in 1936. These figures must be regarded as the lower limits in the present state of our knowledge, and it is clear that Walden does not quite attain this rank, although it approaches it more closely than any other small New England lake yet studied.

Transparency

One of Walden's major charms for Thoreau lay in its exceptional clearness—he found that "the water is so transparent that the bottom can easily be discerned at the depth of twenty-five to thirty feet" (13). It was impossible to corroborate this determination in 1939, as the Secchi disc was not lowered until late in the afternoon, in a part of the lake made noticeably turbid by the activities of nearly a thousand Sunday bathers. The reading of 6 meters is obviously not reliable under these circumstances, but that the lake is unusually transparent is made certain by the fact that living specimens of *Fontinalis* came up with the sounding weight from depths as great as 15.7 meters. This moss is presumably the "bright green weed .... brought up on anchors even in midwinter" (14). Thoreau also records aquatic vegetation from below 12 meters in White Pond, and his queried identification (15) of the plant as *Nitella gracilis* is no doubt substantially correct.

Observations of much greater depths for "rooted" plants are of course on record; Hasler (16) has recently noted water mosses from 120 meters in Crater Lake, Oregon, but casual records indicate a maximum depth of only 12 meters for the growth of vetetation in Connecticut lakes.

The color of the water is 5 (on the U. S. G. S.

scale) throughout the lake except in the bottom layer; this lack of appreciable contamination by allochthonous organic matter is largely responsible for the high transparency (17).

Nutrient content

The mean of two determinations, in July and August, 1939, shows the total phosphorus content of the surface waters of Walden to be very low, 11.5 mg. per cu. m. This condition may be partly due to the fact that the lake is fed solely by ground water, but the regional lithology is such that Concord lakes may be expected to resemble those of the Connecticut highlands in being oligotypic for phosphorus. The above figure is below the mean content of forty-nine Connecticut and New York lakes, and falls between the regional means for the Eastern and Western Highlands (2). The soluble phosphorus was not measured.

The mean surface nitrate content is 20.5 mg. per cu. m. In default of more extensive data this figure has no great significance, as the supply of available nitrogen fluctuates through wide limits during the summer. The potential nitrogen endowment of a lake can sometimes be estimated from the winter nitrate, but no winter analyses are available for Walden.

Biological productivity and oxygen deficit

That Walden is a relatively unproductive lake was appreciated by Thoreau, who observed the scanty crop of littoral vegetation, the absence of organic sediment except in the deepest water (where he correctly attributed its existence to decomposing forest leaves), and the "purity" of the water. He also realized that food chains are thus affected, "you think that they must be ascetic fish that find a subsistence there" (18); and he points out that the larger but comparatively shallow Sandy Pond (Flint's Pond) supports an abundance of aquatic vegetation, is "not remarkably pure," and "is more fertile in fish" (19).

Walden water is indeed "pure" in respect to its plankton content. Plankton counts have not been made, but two analyses of the chlorophyll present in the surface water give a mean value of 3.64 mg. per cu. m. (20), and the Forel-Ule color of the lake is 3. Walden thus closely resembles the lakes of the Eastern Highland of Connecticut in its summer phytoplankton crop (2). The total seston has been estimated gravimetrically from the residue after filtration through a 35-second membrane filter, and found to be extremely low, 0.5 mg. per liter; the amount of ash in this amount of seston was not detectable, so that the same figure represents the organic matter in the seston. No quantity as low as this has been recorded from twenty-four Connecticut and New York lakes, but Birge and Juday (21) report values as low as 0.23 mg. per l. for centrifuge plankton, which is comparable to the membrane filter residue, in northeastern Wisconsin lakes. Expressed on an areal basis, the observed plankton crop amounts to 0.65 mg. per sq. cm., or 65 kilos per hectare, but this can not safely be taken as an average productivity.

The oxygen curve, as shown in Fig. 4, is essentially of the oligotrophic type; the total oxygen content of the hypolimnion is nearly as great as that of the epilimnion, the ratio O_2H/O_2E being 0.73. The curve is further characterized by a maximum in the thermocline. The latter feature gives additional evidence of the transparency of the lake, since such maxima are commonly produced by the photosynthetic activity of phytoplankton organisms concentrated below the epilimnion in the hydrodynamically more stable thermocline, and are not found in lakes in which the compensation point normally lies at a higher level (22).

The oligotrophic form of the curve may with some justice be attributed to the relatively large volume of the hypolimnion, and it is necessary to calculate the areal hypolimnetic oxygen deficit in order to evaluate the fundamental productivity of the lake from the oxygen data (23). Taking the hypolimnion as beginning at 10 meters, and assuming the vernal circulation to have begun on April 1 (Thoreau's average date (24)), the oxygen deficit observed on August 6 appears to have been generated at the rate of 0.0173 mg. per sq. cm. of hypolimnion surface per day, or 0.52 mg. per sq. cm. per month. This single determination of the increment is not altogether reliable, since estimates of the deficit in small lakes, particularly in those of unusual transparency, tend to be minimal (25); but when taken in conjunction with the low standing crop of plankton, the calculation indicates that Walden is a mesotrophic lake. This fact might have been predicted from the geologic similarity between the Massachusetts upland and the Connecticut highlands. Walden, like the lakes of the latter provinces, is unproductive by comparison with those of southeastern Wisconsin (23), or the Connecticut Valley Lowland (2), but

more productive than the mountain lakes of Norway (26).

Alkalinity and iron

The surface bicarbonate content of Walden (9.7 mg. per l) is very low, as might be expected in a seepage lake, and this fact serves to rank it as a soft-water lake. A statistical examination of Connecticut lakes makes it seem highly probable that low alkalinity has no adverse effect on phytoplankton production (2).

Walden resembles other mesotrophic and oligotrophic lakes in the uniform character of its alkalinity curve (Fig. 4); eutrophic lakes (for example, Linsley Pond, Connecticut) frequently show a rise in bicarbonate content in the hypolimnion, due to the acquisition of ferrous and other non-alkali bicarbonates from the mud and their delivery to the open water by density currents (27). The low content of total iron, as shown in Table 2, also demonstrates that this process is quantitatively unimportant in Walden.

TABLE 2
Total iron

DEPTH	Fe
0 m.	0.045 mg./l
20	0.00
25	0.00
30	0.30

Bottom fauna

Although the examination of Walden was made too early in the season to obtain limiting values of the oxidation-reduction potential, the above facts enable one to affirm that the typical Chironomid larva of the profundal zone should be either a species of *Tanytarsus* or the "mesotrophic *Chironomus*" found in similar lakes in Connecticut (28). Analysis of two Ekman bottom samples from 28.2 and 23 meters indicates that the character-form is "mesotrophic *Chironomus*." This larva lacks the ventral blood gills regarded as characteristic of the genus *Chironomus* by Lenz (29), and is known to occur on the bottoms of lakes showing values of the redox potential intermediate between those of typical *Tanytarsus* and typical *Chironomus* lakes (28).

Reliable conclusions as to the abundance of bottom organisms can not be drawn from the two samples taken, but the data appear to reflect a low to moderate benthic productivity. In addition to *Chironomus*, all instars of which were present in the 23-meter sample, the observed fauna comprises several Chironomid larvae of the sub-family Tanypodinae, a few larvae and pupae of *Chaoborus*, and some Tubificid Oligochaets. Cyst capsules characteristic of the Harpacticid copepod *Canthocamptus staphylinoides* were frequent (30), but none appeared to be occupied. No molluscs were encountered, nor were any *Tanytarsus* tubes found.

The sediment of the profundal zone is a typical ooze, and the washed samples contain a high proportion of fragments from the leaves of deciduous forest trees. The presence in the residues of a small amount of carbon, evidently derived from the soot of passing locomotive engines, would have been interesting but scarcely surprising to Thoreau, who resented the intrusion of the nearby railroad.

Limnological summary

Walden Pond, an unusually deep soft-water seepage lake in the Massachusetts upland, is exceptionally transparent, acquires a large amount of heat during the summer season, and closely resembles the lakes of the Connecticut highlands in its low phosphorus content, low plankton crop, and generally low biological productivity. The oxygen curve reflects an oligotrophy (or mesotrophy) which is in part of morphometric and in part of edaphic character. The quantitatively moderate bottom fauna is dominated by "mesotrophic *Chironomus*" larvae. Many limnologically important facts about Walden were first stated by Thoreau.

THOREAU'S PLACE IN SCIENCE

Thoreau's supremacy as an observer of nature among American men of letters has never been seriously questioned since the publication of *Walden*, and even John Burroughs, who complains of the lack of originality in his master's ornithology, finds much to admire in his descriptions. It is strange, therefore, that most of his critics, and, one must suppose, most of his readers, have confined their attention to other facets of his many-sided genius. Leaving aside the other biographies and critical studies, it is sufficient to recall that Canby, perhaps the most discerning and certainly the most widely-informed of Thoreau's biographers, finds his present-day importance to lie chiefly in his moral criticism (31).

It is true, as Canby says, that Thoreau speaks with a homely and original eloquence to readers of many sorts, so that many biographies of the Yankee "hermit" could be written, each with a different and defensible point of view. The biologist, however, must be expected to feel his attraction principally in the sphere of his natural science, and to assess his significance from the lectern of special knowledge.

It has been shown that Thoreau's curiosity was unusually fruitful when directed toward lakes; it is remarkable that this fact appears to have escaped the notice, not only of historians of limnology (32), but of his scientific contemporaries. Limnology, as a separate science, is usually considered to begin with the work of Forel, in 1868, and, except for scattered reports primarily of a taxonomic nature, American limnology was not properly established until after 1890. Thoreau's observations, at least those embodied in *Walden*, were published in 1854, so that the Concord individualist may with justice be called the first American limnologist. His independent discovery of thermal stratification remained in manuscript until 1906, but in any case was antedated by the work of DeSaussure, de la Bèche, Brunner and Simony, who had elucidated the fundamental principles of the temperature distribution in lakes during the latter third of the eighteenth and first half of the nineteenth centuries (33).

The neglect of Thoreau's writings by the scientific world is undoubtedly due to a pardonable distrust of his philosophy. Although he was a corresponding member of the Boston Society of Natural History, an enthusiastic botanist, and a friend of Louis Agassiz, Thoreau never thought of himself as a scientist, but rather as "a mystic, a transcendentalist, and a natural philosopher to boot" (34). According to Sanborn, while Agassiz enjoyed Thoreau's society, "the poet avoided the man of science, having no love for dissection" (35). His works abound in impatient references to the desiccated concepts and vestigial insight of science; in a revealing passage in his *Journal* he rejects what would now be called "phototropism" as an explanation for the turning of plants toward the sun, preferring a more mystical causality (36). "I hate museums," he says, "they are the catacombs of nature" (37). "The inhumanity of science concerns me, as when I am tempted to kill a rare snake that I may ascertain its species. I feel that this is not the means of acquiring true knowledge" (38). "What sort of science is that which enriches the understanding, but robs the imagination? . . . Just as inadequate to a pure mechanic would be a poet's account of a steam engine" (39). "Which are the truest, the sublime conceptions of Hebrew poets and *seers*, or the guarded statements of modern geologists, which we must modify or unlearn so fast" (40)? Such sentiments show as clearly as his more intricate paragraphs Thoreau's largely unconscious kinship with German romanticism (41); they represent a reverberation of *Naturphilosophie*.

Although his thought is steeped in an idealism which the modern biologist can only regard as unfortunate, Thoreau's wide-ranging observation embraced much that was new, and his reflections frequently are cautious, objective, and ingenious; he was a genuine scientist, if only at intervals. As he was a "self-appointed inspector" of the Concord environment, his science as a rule is more distinguished for its scope than for its profundity. His researches led him into such diverse disciplines as plant ecology, systematic botany, animal behavior, ichthyology, anthropology, and geomorphology, in addition to limnology. Yet his versatility, even though hampered by a meager technical facility, did not result in a futile expenditure of his energies.

Thoreau's botany has usually been regarded as his chief claim to scientific eminence. But it is as a plant ecologist, not as a systematist, that this claim is justified. It seems strange that he first made the acquaintance of *Rhododendron nudiflorum* in 1853 (42); in reading the *Philosophia Botanica* of Linnaeus, however, his interest was principally aroused by the ecological classification of plant habitat (43). In one of the last lectures delivered before his death he spoke to the Middlesex Agricultural Society on "The Succession of Forest Trees"; though he overemphasized the reversibility of plant succession, having observed that pine forests usually succeed oak after cutting, his conclusions remain essentially unaltered after sixty years of intensive labor by competent botanists. His view of the dynamics of plant succession was not confined to short-term processes. He not only plumbed the depths of all the bogs known to him, realizing that they were merely senescent lakes, but correctly ascribed the formation of the floating mat to ericaceous shrubs as well as to *Sphagnum* (44). While Thoreau can not be said to have introduced the subject to science, it appears that no important studies of ecological succession were made in America for more than thirty years after his memorable lecture (45).

Many notes on forestry problems made after

the delivery of the lecture are incorporated in the *Journal*, and the last volume is notable for a remarkably acute investigation of the growth of the pitch pine (46). Thoreau appreciated fully the uses of tree-ring analysis, and although the growth curves constructed from his data appear to have remained in his head, he understood their value in ascertaining the most productive period in the life of a stand. It is probable that such studies were meant when he wrote to a correspondent, "if I were to live, I should have much to report on Natural History generally" (47).

These truly scientific observations, and many more of equally astonishing perception, were made by a "poet-naturalist," a disciple of Emerson, and an accepted member of the Concord coterie of transcendentalists. This paradox implies either that he was alternately scientist and mystic, or that being both, he was neither. It has been said that "if Emerson had not spoiled him, Thoreau would have made a good naturalist" (48). On the other hand, Canby expresses the opinion that after the years at Walden, Thoreau was increasingly drawn toward science, but that he was unfortunate in falling under the influence of Agassiz, a taxonomist (49). This view fails to do entire justice to the promulgator of the Glacial Theory, a superb naturalist whose thinking was no less philosophical than Darwin's (50). But at bottom Thoreau's scientific difficulties were of his own contriving, and it is unfair to suggest that he was subverted by anyone. If he mistook the means of scientific observation for its end, and thus remained blind to the advantages of technique, the fault lay partly in the formal curriculum of Harvard College, and partly in his innate distaste for empiricism. Were all such speculations not idle, one might agree with Canby that the world lost a first-rate scientist when Thoreau did not go to Yale, and thus failed to meet Benjamin Silliman.

It is clear, however, that Thoreau's philosophy underwent a change as the habit of observation became more fixed, and the later *Journal* reveals a mind increasingly preoccupied with nature for its own sake and emancipated from the search for an esoteric truth. This alteration is merely implicit; murmurs of the Over-Soul can be detected as plainly in the later writings as in the earlier, and as late as 1860 he announced "I *am* in the lecture field—but my subjects are not *scientific*—rather transcendental and aesthetic" (51). But such statements decrease in number toward the end of his life, and it seems likely that only his premature death obstructed a "working synthesis of science and Transcendentalism" (52). In its diversion from occultism toward nature Thoreau's career offers a refreshing contrast to that of many able scientists. Canby contends that the *Journal* represents the unfinished note-sheets for a monumental contribution to geography, based on an exhaustive study of the natural history of man in Concord (53). This task, as Thoreau conceived it, was superhuman, and scarcely to be accomplished by a man who died at forty-four.

But if it be admitted that Thoreau's mysticism is indefensable, and his science handicapped by his unwillingness to use a valid methodology, his works can nevertheless appeal to a wide biological audience. In his vigorous description of natural phenomena Thoreau stands almost without a peer, and modern biological literature would gain much by emulation of his style and diction. Science has devised no substitute for the charm of his locution, as when he says "thus in the course of ages the rivers wriggle in their beds, till it feels comfortable under them" (54), or speaks of the "maple succeeding because it does not mind a wet foot" (55). A pearl is for him "the hardened tear of a diseased clam, murdered in its old age" (56), and he discusses the "solvency of sand banks" (57). In a noteworthy example of his wit, he pays his respects to those who "believe in the bottomlessness of a pond without taking the trouble to sound it"; "Some who have lain flat on the ice for a long time, looking down through the illusive medium, perchance with watery eyes into the bargain, and driven to hasty conclusions by the fear of catching cold in their breasts, have seen vast holes 'into which a load of hay might be driven,' if there were anybody to drive it, the undoubted source of the Styx and entrance to the Infernal Regions from these parts. Others have gone down from the village with a 'fifty-six' and a wagon load of inch rope, but yet have failed to find any bottom; for while the 'fifty-six' was resting by the way, they were paying out the rope in the vain attempt to fathom their truly immeasurable capacity for marvellousness" (58).

Thoreau's pages are made vivid by such sentences, and although many passages have become classic, for example those dealing with his encounter with the woodchuck and the compotation of the bullfrogs, and have found their way into compilations, the best of him, after *Walden*, is still to be found only in the *Journal*. No natural scientist need be so offended by Thoreau's perverse misunderstanding of the function of science as to neglect him. While the Yankee philosopher,

largely by accident and in spite of his philosophy, occasionally surpassed his more stolid contemporaries at their own profession, the modern reader will rank him with Sir Thomas Browne and W. H. Hudson as a highly gifted amateur, whose scientific achievements are not to be despised because they were intermittent, and related in imaginative prose.

LIST OF LITERATURE

References to Thoreau's "Journal" and to "Walden" are to the *Walden Edition* of his works (*Boston* and *New York*, Houghton Mifflin Co., 1906) in 20 volumes, of which Volumes 7 to 20 contain the "Journal," edited by Bradford Torrey.

(1) BURROUGHS, JOHN: Henry D. Thoreau. *In* Indoor Studies. *London*, J. M. Dent and Co., 1895, pp. 1–42.

(2) DEEVEY, E. S.: Limnological studies in Connecticut. V. A contribution to regional limnology. *American Journal of Science*, Vol. 238, pp. 717–741, 1940.

(3) Note by H. W. GLEASON, appended to map in Thoreau's Journal, Vol. 20, following end of text.

(4) Walden, (Walden edition, Volume 2), p. 319.

(5) *Ibid.*, p. 321.

(6) *Ibid.*, p. 201.

(7) *Ibid.*, p. 319.

(8) *Ibid.*, p. 331.

(9) Journal, Vol. 20, p. 60.

(10) *Ibid.*, p. 66.

(11) BIRGE, E. A.: The heat budgets of American and European lakes. *Trans. Wisconsin Acad. Sci., Arts, and Lett.*, Vol. 18, pp. 1–47, 1915.

(12) TRESSLER, W. L., and R. BERE: A limnological study of some lakes in the lower Hudson area. *N. Y. State Cons. Dept., Ann. Rep.*, Vol. 26 (Suppl.); *Dept. Biol. Surv.*, No. 11, pp. 249–263, 1937.

(13) Walden, p. 197.

(14) *Ibid.*, p. 199.

(15) Journal, Vol. 9 (March 11, 1852).

(16) HASLER, A. D.: Fish biology and limnology of Crater Lake, Oregon. *Jour. Wildlife Management*, Vol. 2, pp. 94–103, 1938.

(17) JUDAY, C., and E. A. BIRGE: The transparency, the color, and the specific conductance of the lake waters of northeastern Wisconsin. *Trans. Wisconsin Acad. Sci., Arts, and Lett.*, Vol. 28, pp. 205–259, 1933. See also Deevey, E. S., Reference 2.

(18) Walden, p. 197.

(19) *Ibid.*, p. 216.

(20) RILEY, G. A.: The measurement of phytoplankton. *Int. Rev. ges. Hydrobiol. u. Hydrogr.*, Bd. 36, s. 371–373, 1938.

(21) BIRGE, E. A., and C. JUDAY: Particulate and dissolved organic matter in inland lakes. *Ecol. Mon.*, Vol. 4, pp. 440–474, 1934.

(22) YOSHIMURA, S.: Stratification of dissolved oxygen in a lake during the summer stagnation period. *Int. rev. ges. Hydrobiol. u. Hydrogr.*, Bd. 38, s. 441–449, 1939.

(23) HUTCHINSON, G. E.: On the relation between the oxygen deficit and the productivity and typology of lakes. *Ibid.*, Bd. 36, s. 336–355, 1938.

(24) WALDEN, pp. 330, 334.

(25) RILEY, G. A.: Limnological studies in Connecticut. I. General limnological survey. *Ecol Mon.*, Vol. 9, pp. 53–66, 1939.

(26) STRØM, K. M.: Limnological observations on Norwegian lakes. *Arch. Hydrobiol.*, Bd. 21, s. 97–124, 1930.

——: Feforvatn. A physiographical and biological study of a mountain lake. *Ibid.*, Bd. 22, s. 491–536, 1931.

——: Lilla Le. A preliminary survey of a remarkable lake. *Geograf. Ann.*, 1932, pp. 259–272.

(27) HUTCHINSON, G. E.: Limnological studies in Connecticut. IV. The mechanisms of intermediary metabolism in stratified lakes. *Ecological Monographs*, Vol. 11, pp. 21–60, 1941.

(28) HUTCHINSON, G. E., E. S. DEEVEY, and A. WOLLACK: The oxidation-reduction potentials of lake waters and their ecological significance. *Proc. Nat. Acad. Sci.*, Vol. 25, pp. 87–90, 1939.

(29) LENZ, F.: Chironomidenpuppen und Larven. Bestimmungstabellen. *Deutsch. Entomol. Zeit.*, 1921, s. 148–162.

(30) MOORE, G. M.: A limnological investigation of the microscopic benthic fauna of Douglas Lake, Michigan. *Ecol. Mon.*, Vol. 9, pp. 537–582, 1939.

(31) CANBY, H. S.: Thoreau. *Boston*, Houghton Mifflin Co., 1939, 508 pp.

(32) WELCH, P. S.: Limnology. *New York* and *London*, McGraw-Hill, 1935, 471 pp.

(33) DE SAUSSURE, H.-B.: Voyages dans les Alps. *Geneva*, 1779–1796. (Especially I, Ch. 2, and V., Chap. 2).

DE LA BÈCHE, H. T.: On the depth and temperature, etc. *Bibliotheque Universelle des Sciences, Belles-Lettres, et Arts*, T. 12 (Sci. et Arts), pp. 118–126. *Geneva*, 1819.

BRUNNER, C.: Recherches sur la temperature du lac de Thoune. *Mem. Soc. Physique et d'Hist. Nat. Genève*, T. 12, pp. 255–276, 1849.

SIMONY, F.: Die Seen des Salzkammergutes. *Sitzber. d. math.-nat. Classe d. k. Akad. d. Wiss., Wien*, Bd. 4, s. 542–566, 1850.

(34) Journal, Vol. 11, p. 4.

(35) SANBORN, F. B.: Henry D. Thoreau. (American Men of Letters) *Boston* and *New York*, Houghton Mifflin Co., Revised Edition, 1910, pp. 244–245.

(36) Journal, Vol. 18, p. 23.

(37) *Ibid.*, Vol. 7, p. 464.

(38) *Ibid.*, Vol. 12, p. 311.

(39) *Ibid.*, Vol. 9, p. 156.

(40) *Ibid.*, Vol. 20, p. 117.

(41) MORE, P. E.: Thoreau's journal. *In* Shelburne Essays, Fifth Series, *Boston* and *New York*, Houghton Mifflin Co., 1910, pp. 106–131.

CRAWFORD, B. V.: Henry David Thoreau. Representative Selections, with Introduction, Bibliography, and Notes (American Writers Series). *New York*, American Book Co., 1934.

(42) Journal, Vol. 11, pp. 204–209.

(43) *Ibid.*, Vol. 9, pp. 346–348.

(44) *Ibid.*, Vol. 16, pp. 201, 269, 271–2.

(45) CLEMENTS, F. E.: Plant succession. An analysis of the development of vegetation. *Carn. Inst. Wash.*, Pub. No. 242, 512 pp., 1916. Mr. J. W. Hechinger, however, states in a personal communication that he has found four references to American work in this field, published before 1850.

(46) Journal, Vol. 20, pp. 232–239.

(47) CANBY, H. S.: *Op. cit.*, p. 433.

——: The Works of Thoreau. *Boston*, Houghton Mifflin Co., 1937, p. 641.

(48) CANBY, 1939, p. 324.

(49) *Ibid.*, pp. 324–330.

(50) MARCOU, J.: Life, Letters, and Works of Louis Agassiz. *New York* and *London*, Macmillan and Co., 2 vols., 1896.

(51) CANBY, 1939, p. 431.

(52) *Ibid.*, p. 324.

(53) CANBY, 1937, pp. xv–xvi, 1939, pp. 334–336.

(54) Journal, Vol. 13, p. 268.

(55) *Ibid.*, Vol. 20, p. 323.

(56) *Ibid.*, Vol. 16, p. 7.

(57) *Ibid.*, p. 93.

(58) Walden, pp. 315–316.

CONTROL OF SWIMMING POSITION BY MECHANICAL FACTORS AND PROPRIOCEPTION

By JOHN H. LOCHHEAD

The Biological Laboratories, Harvard University, and The Zoölogical Laboratory of the Johns Hopkins University

(Now at Virginia Fisheries Laboratory, College of William and Mary, Williamsburg, Va.)

IT IS a well-known fact that most types of free-swimming Metazoa swim in characteristic positions. The body has usually a dorsal and a ventral surface, and the more typical animals swim with the back directed upwards. Some forms adopt the opposite position, with the back directed downwards, and there are various other orientations characteristic for certain species.

In many cases the normal position is maintained by an active reflex mechanism, which may be associated either with statocysts or with a response to light. Light, however, is often absent, and there are a large number of invertebrates in which statocysts have not been found. Proprioceptive orientation might occur, or orientation based on some special sensitivity to currents, but as yet we have no adequate evidence to support these possibilities.

It is particularly in the absence of any reflex orientation to stimuli that purely mechanical forces may be important for controlling the swimming position of an aquatic animal. In the present paper the discussion will center mainly on the various types of such mechanical orientation which theoretically might occur. The possible rôle of proprioception will be discussed briefly towards the end.

Although a large number of authors have appreciated that mechanical forces may be concerned in the swimming position of an aquatic animal, attempts to analyse these forces have not been satisfactory. There has been some valuable work on such topics as propulsive mechanisms and directional stability (see, for example, papers on fish by Magnan, 1929, 1930; and by Harris, 1936, 1937, 1938). But very little has been done on the mechanical factors which would favor return to a stable position. Perhaps the best papers in this field are those of Bethe (1894, 1910) and Woltereck (1913). These, however, do not give a complete picture, and most later authors have underestimated the complexity of the problem, frequently reaching conclusions which were not justified by the experimental evidence available. There appears to be a real need for a simple statement of the nature of the problem, if for no other reason than to serve as a gentle caution. To supply this need it seems best to make the treatment as elementary as possible, perhaps to the disappointment of those who have any real appreciation of aero- or hydrodynamics.

POSSIBLE IMPORTANCE TO THE ANIMAL

At the outset it is perhaps appropriate to enquire what features of importance a stable position may possess for the swimming animal. One of the most obvious of these is to be seen when the specific gravity of the animal is greater than that of the water in which it lives. Such an animal will tend to sink, and this tendency must be resisted by some mechanism, for which it is important that the animal remain orientated with the correct side up. If the body becomes turned upside down the mechanism will act the wrong way, unless the animal is able to perceive its predicament and to reverse the mechanism.

Another important effect of a stable body position concerns the angle or direction of the swimming path in relation to the horizontal. If the body tends to lie in one particular position, any chance tip of the anterior end up or down will automatically be corrected, unless special steering organs are employed. The swimming path will thus remain at a more or less constant angle to the horizontal, with certain advantages to the animal which the ecologist will readily recognize (see, for example, Woltereck, 1913). From the normal

path the animal should be able to steer up or down at will, following some chosen direction with respect to the horizontal, without any need for a special sense to aid in orientation.

When the mechanically favored path is more vertical than horizontal the animal may appear to show positive or negative geotaxis. This fact has been recognized by former authors, and indeed mechanical control forms the basis of one of the theories advanced to account for geotaxis, as listed by Parker (1922) and by Dembowski (1929). It may be noted, however, that the theory has rarely if ever been found to supply the whole explanation for geotaxis in a given aquatic animal, although in the case of the ciliate, *Paramaecium*, Dembowski (1931) has found that the theory will hold under certain special conditions.

In many animals the position of the body may affect not only the vertical inclination of the swimming path but also the directional stability for turns in the horizontal plane. This is particularly obvious in the case of animals which are laterally compressed. Typically there are certain vertical surfaces which offer a resistance to any tendency on the part of the animal to deviate to the left or right. If, however, the body tips over onto one side, these surfaces can no longer offer this resistance, and directional stability in the horizontal plane will probably be much reduced. The matter can be one of some importance to the animal because to wander in circles in a horizontal field may reduce the opportunities for finding fresh food, a mate, or other necessities in the environment.

For some animals it is possible that maintenance of the normal body position is of direct importance for health. If the animal were to lie too long in an abnormal position, there might be changes in internal organization, or some interference with organic function. Parr (1927) and Breder and Harris (1935–6) have claimed that this may actually be the case in certain fish.

For aquatic animals which live near the surface, or near the bottom, there may be yet other ways in which the maintenance of a stable swimming position can be significant, in connection with functions such as feeding and respiration. In some cases it is possible that animals swimming at intermediate depths may be able to catch sinking food particles better when lying in one position than when in another. Indeed for a majority of the free-swimming animals there are probably several ways in which the swimming position is of importance, depending on the habits and environment of the species concerned.

It must be understood, however, that mechanical stability of position need not be wholly advantageous. If this were so we might expect that all swimming animals would be specially weighted along the lower surface. Such is not the case, probably largely because of the fact that too much stability reduces the ease with which the animal can manoeuvre. Some animals may be designed something like the modern transport aeroplane, with good stability, but without the capacity for turning rapidly in every direction. Others, more particularly those of more complex organization, will probably be much more like the fighting aeroplane, having the mechanical stability largely replaced by nervous control, and with well developed powers of turning rapidly in every sense required. In the case of fish it is known that many species rest in a position of slightly unstable equilibrium, maintaining the delicate balance by constant movements of their fins. It is tempting to suggest that the need for constant balancing has some survival value, serving to keep the fish alert, and ever ready for rapid movements in any direction.

BASIC TYPES OF MECHANICAL ORIENTATION

The forces which act upon the body of a swimming animal may be arranged in various ways. If the animal swims in some constant orientation relative to the axes of the earth, it is probable that this position will be one of equilibrium, in which all the forces balance. A chance rotation away from this orientation will disturb the balance, with the result that the body will either tend to rotate further, or will return to the original position. In the present section of this paper a discussion will be presented of the various arrangements of forces which might serve to control and maintain such a constant orientation. To simplify the problem the discussion will be illustrated by reference to simple geometrical bodies, rather than to the more complicated conditions which occur in actual animals.

The type of mechanism which first springs to mind is one in which the center of gravity tends to lie beneath a center of support. When the body is one with a specific gravity equal to that of the surrounding water, the support is wholly provided by the upward force of "buoyancy", acting through the center of buoyancy or center of mass of the displaced liquid, and equal in magnitude to the weight

of this liquid. If the body is of uniform density its centers of gravity and buoyancy will coincide, and it will float submerged in any position in a state of indifferent equilibrium. If, however, the body is not of uniform density the center of gravity will probably be displaced and the body will tend to float with this center vertically below the center of buoyancy (Fig. 1). Any chance rotation away from this position would establish a torque between the upward force of buoyancy and the downward pull of gravity, tending to restore the former position. Turned upside down the body would be in a position of unstable equilibrium, which could be maintained only by some system of careful balancing (as actually occurs in many kinds of fish).

The principle of the mechanism was clearly recognized by Borelli (1681), and it has since been well described by other biologists, such as Bethe

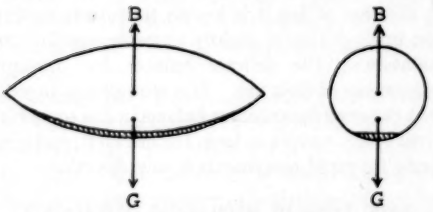


FIG. 1. LONGITUDINAL AND TRANSVERSE SECTIONS OF A BODY WITH TOTAL SPECIFIC GRAVITY EQUAL TO THAT OF THE SURROUNDING WATER

Shaded part denser than the rest. G and B represent the forces of gravity and buoyancy.

(1894, 1910), Müller (1919), and Magnan (1930). Yet the earlier paper by Bethe contains the statement that if a cone is thrown into a vacuum it will fall with the heavy end directed downwards. Although quite erroneous this statement has been quoted by some more recent authors (e. g. Magnus and de Kleijn, 1930), and it has perhaps led several other authors to express the view that the center of gravity will always tend to lie "as deep as possible", without giving any indication as to what point would tend to lie above it (Williams, 1900; Dembowski, 1929; Lowndes, 1937; in part also Alverdes, 1927; and Bethe, 1894, 1895). It must be pointed out that the force of gravity alone is not sufficient to produce orientation; in the simplest case there must be at least one other force, directed upwards, and not acting through the center of gravity except when the body is in a position of stable (or unstable) equilibrium.

The mechanism illustrated in Fig. 1 is of particular importance for bodies which have a specific gravity equal to that of the surrounding water. If opposing forces are absent such a mechanism will work almost equally well whether the body is stationary or moving, and it can also be effective when the body is of a specific gravity which is greater or less than that of the surrounding medium. In the latter cases, however, other forces usually become involved, and these may essentially alter the position of stable equilibrium.

Among free-swimming invertebrates there are many which have bodies with a specific gravity greater than that of the water in which they live. The force of buoyancy being thus insufficient to prevent sinking, the animals must provide some further support, either as a vertical component of the propulsive force, or as "dynamic lift" of the type which enables aeroplanes to fly.

It might be thought that under these conditions there would be a tendency for the center of gravity to lie underneath a new center of support, and indeed such a view has been expressed by some authors who have written on the flight of birds, of whom Borelli (1681) was probably the first. Plate (1924) advances the same view for animals which either fly or swim.

The requirements of this view would be met partially if we imagine an animal provided with appendages which within certain limits would automatically beat downwards, even if the body were tipped over to one side. This result might be achieved by having a certain degree of tension or elasticity in the basal parts of the appendages, allowing a graded amount of bending in response to the resistance of the water (Fig. 2). Under these conditions it would be possible to speak of an approximate center of support, lying between the two appendages, and of a tendency for the center of gravity to lie below this point. If, however, the body were turned more nearly upside down, the appendages could no longer beat downwards and the animal would probably sink helplessly, unless it was able to perceive the situation and to make the necessary reflex adjustments.

Among living animals it is doubtful if any examples can be found which possess a mechanism of the type just described. Certainly in the great majority of cases any upward force exerted by the animal is fixed in direction relative to the animal and not relative to the axes of the earth. If the animal tips over, away from the normal position,

the force will no longer act upwards to the same degree, unless the animal changes the mode of action of the propulsive organs. This means that it is no longer correct to speak of a tendency for the center of gravity to lie beneath a center of support. In fact the term "center of support", or "center of action of the supporting force", loses its meaning when the direction of this force is fixed relative to the body of the animal. A line of action for the force can be defined, but not a point of action, animal should have a specific gravity which is not equal to that of the surrounding water.

Some of the general principles involved can be illustrated by reference to an imaginary spherical organism, heavier along one side than elsewhere, and propelled through the water by a propulsive force, P. To simplify the problem let it be supposed that the relative force of buoyancy is so small that it can be neglected. The body will then be acted upon by the downward force of gravity,

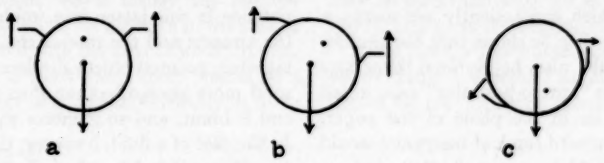


FIG. 2. TRANSVERSE SECTION OF IMAGINARY ANIMAL PROVIDED WITH APPENDAGES WHICH PRODUCE A FORCE AUTOMATICALLY DIRECTED UPWARDS (a, b), EXCEPT WHEN THE BODY HAS ROTATED OVER TOO FAR (c)

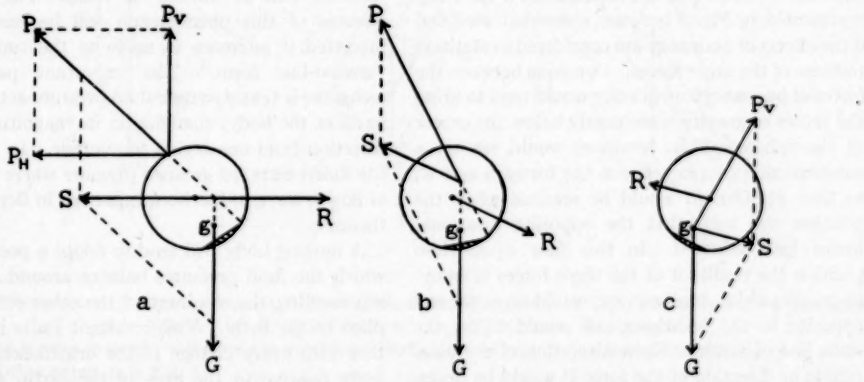


FIG. 3. HYPOTHETICAL SPHERICAL ORGANISM. (a) ANTERO-POSTERIOR SECTION, STABLE EQUILIBRIUM POSITION. (b) DITTO, UNSTABLE POSITION AFTER ROTATION AROUND TRANSVERSE AXIS. (c) TRANSVERSE SECTION, UNSTABLE POSITION AFTER ROTATION AROUND ANTERO-POSTERIOR AXIS

P = propulsive force (P_V and P_H the vertical and horizontal components), G = force of gravity, S = resultant of these two forces. R = resistance. g = center of gravity.

since there is no one point along the line through which the force can be said to act more than it does through any other.

Mechanical control of the orientation of a swimming animal might, however, be achieved in a number of other ways, which do not depend on the presence of a fixed center of support. The mechanisms here concerned are all somewhat complex, involving the interrelationships between at least three forces, those of gravity, propulsion, and resistance. In each case it is essential that the G, and it will be subjected to a net pull, S, representing the resultant of the forces G and P. Let the magnitude and direction of the force P be as shown in Fig. 3a, such that when the resultant force S acts along a line which is horizontal, this line will pass through the center of the sphere. P_V, the vertical component of the propulsive force, would then be equal to G, and the body would be pulled forward horizontally by the force P_H, here equal to S. Opposed to the forward motion there would be a resistance, R, acting through the center

of the sphere, and also through the point of intersection of the forces G and P.

It will be seen that under these conditions the position of the body is one of equilibrium, in which all the forces balance. Any slight rotation around an axis at right angles to the paper would cause a shift in the line of action of the resultant force S, such that a couple would be created between the forces S and R (Fig. 3b). Inspection shows that the rotational force of this couple would always act in a direction tending to restore the former position of equilibrium, which consequently represents a stable orientation. Fig. 3c shows that the equilibrium position would also be restored after any rotations around an "antero-posterior" axis, which in Fig. 3a would lie in the plane of the paper.

Neglect of the upward force of buoyancy would not be justified if the body were really that of a free-swimming animal, since no such animals have specific gravities much above that of the surrounding water. The equilibrium position for the body represented in Fig. 3 becomes somewhat modified if the effects of buoyancy are considered in addition to those of the other forces. A torque between the forces of buoyancy and gravity would tend to bring the center of gravity more nearly below the center of the sphere. This, however, would set up a counteracting couple between the forces S and R, so that equilibrium would be reached when the position was such that the opposing rotational forces just balanced. In this new equilibrium position the resultant of the three forces of buoyancy, propulsion, and gravity, would be equal and opposite to the resistance and would follow the same line of action. Some alteration of the magnitude or direction of the force P would be necessary, if it was desired that the body should continue to progress forward horizontally.

The line of action of the fluid resistance is particularly easy to predict in the case of a sphere, the shape of which is such that the resistance always acts through the center of the body, following a line parallel to the direction of motion. For bodies of other shapes the problem becomes more complicated, because there can be no one point through which the resistance will always act, nor will the line of action of this force necessarily be parallel to the direction of movement. The complications introduced by these facts are difficult to analyze in simple geometrical drawings, but a few general points must be discussed here, since not many animals are even approximately spherical.

At the outset it seems advisable to describe more precisely what is meant by the term "fluid resistance." It is well known that when a body moves through water it meets with a kind of dynamic pressure or resistance which opposes the motion. To some extent such resistance is caused by surface friction. Usually to a much greater extent it is caused by resistance of the water to displacement, and comparison might be made with the situation which would occur if the body were pushed through an easily deformable solid. Resistance in this latter case would depend on both the amount and the rate of the displacement. A tapering, pointed object displaces the surrounding solid more gradually than does one in which the end is blunt, and so it meets with less resistance. In the case of a fluid, however, the situation is profoundly modified by the way in which the fluid closes in behind a moving body. Pressures or resistances thus act behind the body and along its sides as well as directly in front. The consequences of this phenomenon will be easily appreciated if reference is made to the subject of "stream-line form." The important point to recognize is that dynamic fluid pressure acts on all parts of the body, changing in its magnitude and direction from one region to another. In general the fluid exerts the greatest pressure where its rate of flow is least, as has been expressed in Bernoulli's theorem.

A moving body will tend to adopt a position in which the fluid pressures balance around an axis representing the resultant of the other forces applied to the body. This resultant shifts its position with every change in the orientation of the body relative to the axes of the earth, and the problem can be especially complicated when the resultant does not always pass through the center of gravity (as, for example, in Fig. 3). A simpler case is afforded by a body of uniform density sinking passively under the influence of gravity alone. Under such conditions the body would tend to assume a position in which all the forces balanced around a vertical line drawn through the center of gravity. In some cases there might be several such balance or equilibrium positions, but for bodies of some shapes only one of these positions would represent a really stable orientation.

If an attempt is made to predict what this orientation would be for a body of given shape, there is one important general theorem which can be of service, to which the attention of biologists

has been directed by Lowndes (1937). The theorem states that if a body is moving freely through a fluid, under the influence of external forces, it will tend to adopt a position in which a maximum cross-sectional area is placed across the direction of motion. The factors concerned in a simple case are given full mathematical treatment, as well as an explanatory diagram, in Lamb (1924, pp. 82 and 154–6).

But frequently there may be at least two quite different orientations which satisfy the requirements of the theorem, as for instance in the case of an elongated animal with dorso-ventral differentiation. Probably in most cases there would be a tendency to assume one of these orientations more often than the other, and perhaps the favored position would usually be the one offering the least resistance. How far that would be found to represent a general rule seems rather doubtful, but Bethe (1894) probably had such an idea in mind when he claimed that a sinking body will occupy the position which offers the least resistance. His statement is not in agreement with the theorem quoted above, but perhaps it was intended to apply only to the choice of positions which may exist after the requirements of that theorem have been already met.

Turning to consider some concrete examples, we may begin by considering the case of a body which is oval in cross-section, and in which the tendency to sink is resisted by an upward force, P, acting along the longer axis. When the body lies with the pole, p, directed upwards it will neither sink nor rise (Fig. 4a). If it tips over to one side it will become subjected to the resultant force, S, which will pull it sideways and somewhat downwards. The resistance which is met with will be such as to tend to set the body broadside on to the direction of motion, or in other words there will be a couple tending to restore the former position. The same would be true for any further degree of rotation, as may be seen from Figs. 4b and 4c. The position shown in Fig. 4a is thus one of stable equilibrium.

If the force, P, is pulling forwards as well as upwards quite a different situation will exist with regard to the rotations around the "transverse" axis. It can be supposed, for example, that the body seen in transverse section in Fig. 4, is cigar-shaped when seen in longitudinal section. The force, P, can be placed so as to act diagonally through the center of gravity, such that when the longitudinal axis of the body is horizontal the vertical component, P_v, then exactly balances the downward force, W (Fig. 5a). Under such conditions the body would be in equilibrium and would move forward horizontally. A tilt of the nose up or down, however, would cause the resultant of the forces, P and W, to move above the longitudinal axis. The body would now tend to set itself broadside on to the direction of pull, and thus it would rotate in the direction indicated by the curved arrows (Figs. 5b and 5c). It will be seen

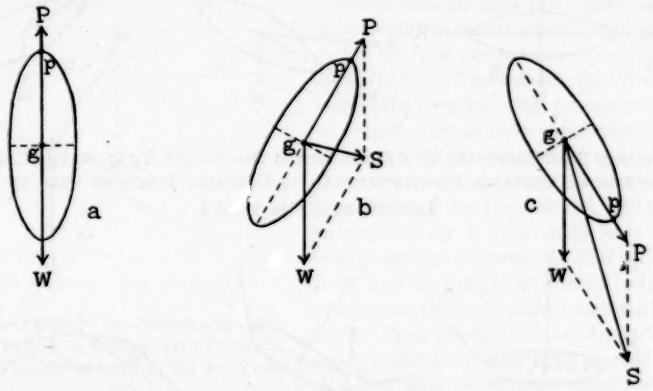


FIG. 4. TRANSVERSE SECTION OF ANIMAL WHICH RESISTS THE TENDENCY TO SINK BY AN UPWARD PROPULSIVE FORCE. (a) STABLE POSITION. (b, c) UNSTABLE POSITIONS

W = force due to weight of the body in water (equal to the force of gravity less that of buoyancy). p = dorsal pole. Other letters as in Fig. 3.

that the direction of rotation is the same in each case, and in fact the body would rotate continuously once it had left the position of unstable equilibrium represented in Fig. 5a. The same would be true for a body of greater height than length, except that the rotations would be in the opposite direction.

Various other possibilities emerge when we consider bodies which are not symmetrical above and below a median horizontal plane. For example the addition of a pair of sloping wings can reverse the stability of a body which is oval in cross-section, and which exerts a force, P, acting along the shorter axis (Fig. 6). Without the wings such a body would not remain in stable equilibrium when the force, P, was directed upwards, but rather it would tend to turn over and sink. With sloping wings attached as shown, the position in which the force, P, is directed upwards becomes one of stable equilibrium, to which the body would tend to return after all except the most extreme degrees of rotation around its longitudinal axis. A more precarious position of stable equilibrium would also exist when the body was turned completely upside down, but the range of rotations over which there would be any tendency for return to this position would be relatively small (Fig. 6c).

Yet another situation is created if the body is supported by a vertical component of the resistance, the so-called "dynamic lift", instead of by a vertical component of the propulsive force. Under these conditions the propulsive force can be arranged to act directly forwards, and at a certain speed of forward movement the upward lift will exactly balance the forces pulling downward. The factors which control stability of orientation are then somewhat different from those which have been described in the examples given above. They can perhaps be illustrated best by reference to the part which they play in controlling the stability of an aeroplane. (A good popular account of stability in aeroplanes is given by v. Mises (1936).)

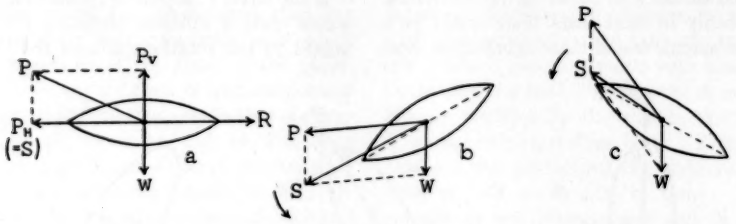


FIG. 5. CIGAR-SHAPED BODY PROPELLED BY A FORCE ACTING DIAGONALLY THROUGH THE CENTER OF GRAVITY. (a) POSITION OF UNSTABLE EQUILIBRIUM. (b, c) UNSTABLE POSITIONS WITH NO EQUILIBRIUM
Lettering as in Figs. 3 and 4

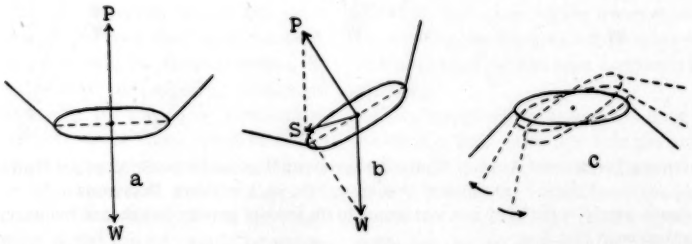


FIG. 6. TRANSVERSE SECTION OF A BODY WITH FIXED SLOPING WINGS, WHICH RESISTS THE TENDENCY TO SINK BY AN UPWARD PROPULSIVE FORCE. (a) STABLE POSITION. (b) UNSTABLE POSITION. (c) POSITION OF LIMITED STABILITY—INDICATED BY BROKEN LINES ARE TWO UNSTABLE POSITIONS, FROM WHICH THE BODY WOULD TEND TO RETURN TOWARDS 'c' AND TOWARDS 'a' RESPECTIVELY.

The orientation of an aeroplane can be disturbed by rotations either around the longitudinal axis or around the transverse axis, and these two types of rotation must be considered separately. For the rotations around the longitudinal axis there are some aeroplanes which are relatively stable, but

there are others which are not. The latter type are constructed with wings which extend out horizontally from the body, so that the wings of opposite sides lie in the same geometrical plane. If an aeroplane of this type tips over to one side while it is flying straight forward at constant speed, the lifting force, L, will continue to act at right angles to the wings and will remain unchanged in magnitude. The aeroplane will thus be subjected to a sideways and downward pull, representing the resultant between the forces L and W (Fig. 7). The resistance which is met will tend to set the aeroplane broadside on to the direction of pull, and since the pull passes above the wing the aeroplane will tend to turn over. The normal flying position is thus one of unstable

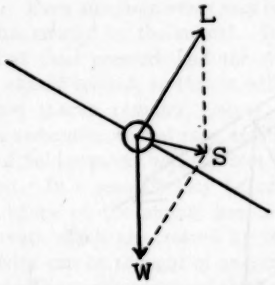


FIG. 7. TRANSVERSE SECTION OF AEROPLANE WITH PARALLEL WINGS FLYING IN AN UNSTABLE POSITION, IN WHICH THE TENDENCY WOULD BE TO TURN UPSIDE DOWN.

L = force of "dynamic lift." W = downward pull due to the weight. S = resultant of these two forces.

equilibrium, which can be maintained only by constant vigilance on the part of the pilot.

It is hardly surprising that in most aeroplanes some attempt is made to change this state of affairs. The method used consists in attaching the wings so that they slope slightly upwards from the body, out towards their free ends. A very small degree of slope is sufficient to ensure considerable stability. If the aeroplane tips over during flight it will start to slip sideways and downwards as described above. Air now meets the lower of the two wings at a greater "angle of attack" than it does the upper wing, and the result of this is a difference in the lift exerted on the two sides, tending to restore the aeroplane to its former position. It may be noted in this connection that the wings usually slope somewhat upwards from back to front (so as to offer a small "positive" angle of attack), and that consequently during forward movement the air usually strikes the lower surface first, even when the aeroplane is slipping sideways under the influence of a pull acting along a line above the wing. It is also of some importance that the shape of the wings, as seen in cross-section, is such that they continue to supply some upward lift even when the angle of attack is slightly "negative."

Another method to ensure stability for rotations around the longitudinal axis would be to provide the aeroplane with enormous median vertical fins, so as to give the sagittal plane a greater area than that which is offered by the wings. There would now be no need for the two wings to slope upwards towards their free ends, since the conditions would be essentially similar to those shown in Fig. 4. The arrangement would not be practicable for normal aeroplanes, but in many aquatic animals a corresponding arrangement may well be found. As has been noted before, the specific gravity of aquatic animals is never much above that of the water in which they live, so that only a small lifting force is required. This force could be supplied by a very small pair of wings, or indeed without any wings at all if the shape of the body and its "angle of attack" were such that pressure on the lower surface exceeded that above. Under these conditions the depth of the body easily might be greater than the width, in which case the type of stability illustrated in Fig. 4 might be present.

Turning now to consider the control of rotations around the transverse axis, it can be shown that in the aeroplane this is largely due to the action of the horizontal tail fin. When flying forward horizontally the aeroplane is subject to a net pull, S, which represents the resultant of the two forces, P and W. This pull is exactly balanced by the resistance, R, and if the aeroplane is correctly "trimmed" the tail fin will be exactly horizontal and therefore not contributing to the lift. If an aeroplane which is trimmed in this way should attempt to fly diagonally downwards or upwards, the direction of the force S will be changed relative to the machine. As a result of this the aeroplane would take up a slightly different angle of attack, thus exposing the tail fin to extra pressure, above or below as the case may be (Fig. 8). It will be seen that these new pressures on the tail are such

as to cause the aeroplane to return to a horizontal course.

Pressures of the same kind are especially well developed during and immediately after any chance departures from a horizontal path. For a few moments the force of inertia causes the machine still to follow that path, although the body is pointed in a new direction. The horizontal tail fin is consequently exposed to a considerable pressure, which tends to restore the machine to its former orientation. If, however, the return to this position is in some way delayed, the aeroplane will start to fly in the new direction, and very soon the pressure on the tail will disappear except for a certain amount which can be attributed to the factors discussed in the last paragraph. The purely momentary pressure which arises during active jumps. If the jumps are directed diagonally upward and the pauses are of a suitable length, the net forward path will be horizontal. A considerable number of aquatic animals exhibit this type of swimming, and an excellent analysis of some of the factors concerned in the case of Cladocera has been given by Woltereck (1913).

It is of interest to note that Bethe (1910) held the opinion that the shape of a swimming animal can be of importance for controlling its orientation only if the progression is discontinuous. Lowndes (1937) has rightly stressed the more general importance of body shape, but he appears to overlook the fact that orientation cannot be controlled by this factor except when the specific gravity of the body is definitely above that of the surrounding water.

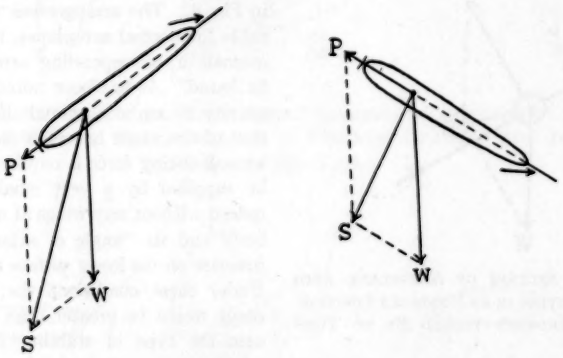


FIG. 8. LONGITUDINAL SECTIONS OF AEROPLANE TRIMMED FOR HORIZONTAL FLIGHT, SHOWN AS ATTEMPTING TO FLY DIAGONALLY DOWNWARDS AND UPWARDS

and after a change of orientation is of great importance for directional stability, but it cannot serve to maintain a body in some constant orientation relative to the axes of the earth.

A comparison of the conditions illustrated in Fig. 8, with those shown in Fig. 5, suggests that stability in regard to rotations around the transverse axis can more easily be attained when support is provided by "dynamic lift," than when it is provided by a vertical component of the propulsive force. In cases of the latter kind, however, the difficulties can be overcome if forward progression occurs as a series of jumps, each one followed by a pause during which the body has time to reach approximately the position seen during passive sinking. An arrangement of this type allows the body to be constantly re-orientated, no matter to what extent the orientation may be lost during the

If an attempt is made to summarize the various ways in which the orientation of swimming animals might be mechanically controlled, it appears that there are perhaps three basic mechanisms which are more likely to occur than any others. The first of these is the mechanism involving a relationship between the centers of gravity and buoyancy. This is the only mechanism possible in animals which have a specific gravity equal to that of the surrounding water. It may also be important in animals with a specific gravity exceeding that of the water, but there are then various other mechanisms possible, of which two seem especially likely to occur. If the animal is one in which the tendency to sink is resisted by a vertical component of the propulsive force, it will probably swim in jumps, allowing its body to be orientated by fluid pressures during the brief periods of passive sink-

ing. If the supporting force is provided by "dynamic lift" the animal will perhaps swim continously and its orientation may be controlled by some mechanism similar to that which exists in the aeroplane.

When efforts are made to apply such theoretical conclusions to actual living animals the difficulties may increase enormously. Reasons for this are, first, the changes in shape so often seen when the animal swims; and, second, the complex system of currents which the animal may create by its own activity. Changes in shape during swimming may essentially alter the effective shape of the animal and its relation to the surrounding fluid pressure. This is a factor difficult to estimate or to test experimentally, but it must be considered when trying to interpret results obtained with non-living material. Even more important may be the effects of currents created by the animal. It was noted above that fluid pressure and the rate of fluid flow are closely related, so that it will readily be understood that a complex system of currents around a swimming animal may greatly alter the pattern of fluid pressure which is met with during movement. In a sense it may be said that the effective shape of the animal has been altered. The currents which are created by the animal's own activity can be thought of as forming a permanent shell or envelope around the body. If the animal starts to sink it is this envelope which meets the water lying ahead, and which determines its lines of flow on being displaced.

SOME EXPERIMENTAL METHODS

An experimental analysis of mechanical factors concerned with orientation in a given animal may sometimes be extremely difficult. Not only may there be complications of the type just described, but the various mechanisms which are possible may be modified or combined together in almost any way. Some of the more complex cases are probably beyond the scope of experimental methods known at present. Nevertheless it should be of some value to review briefly such methods as have been used by previous investigators, or which might be tried in the near future.

To find the position of the center of gravity the simplest method is that used by Magnan (1929). Working with various species of fish he first found the position in which the body would balance horizontally when laid across a sharp edge. He then suspended the animal from one end or from one of the fins. Vertical lines from the points of balance and of suspension were drawn in each case, and the point in the median plane at which these lines crossed was taken to represent the center of gravity. Fish with flexible bodies were laid across the two pans of a balance and the position adjusted until the median pointer remained vertical.

For small invertebrates the problem is more difficult. Müller (1919) describes a method which he used to determine the horizontal balance position in a fairy shrimp (Crustacea Anostraca). He did not, however, attempt to define the position of the center of gravity more precisely.

In all such experiments certain precautions are necessary. The animal should be killed or narcotized in a manner which does not cause local changes in specific gravity. The shape of the body and the contents of the gut must be normal. If the determinations are made in air the surface of the body should be carefully dried, yet at the same time there must be no loss of internal fluids. Some of these difficulties might be avoided if the determinations could be carried out under water. This, however, would not be possible except for animals with a specific gravity considerably above that of the water, and it would require special care to avoid the disturbing action of local currents.

The position of the center of buoyancy can be found by constructing a model of uniform density and then finding the center of gravity of this model. Magnan (1929) employed this method for fish. He also used a method which did not give the exact position of the center of buoyancy, but which showed how far it was in front of or behind the center of gravity. For this purpose a fish was supported under water by a pin which pierced the body transversely through the center of gravity. Small weights were then placed on the back, near this region, and shifted until the long axis of the body came to lie just horizontal. A simple calculation gave the required result.

For small and soft-bodied animals accurate determinations of the positions of the centers of gravity and buoyancy become almost impossible. Usually the best that can be done is to determine the relative positions of these two centers to each other. To do this it is necessary to float the body of the animal in a liquid of a specific gravity equal to its own. If the two centers coincide the body will be in indifferent equilibrium and will float in any position. If the two centers do not coincide there will be a tendency for the center of gravity to lie vertically below the center of buoyancy. Some idea of the distance apart of the two centers

will be indicated by the speed of rotation towards this position of stable equilibrium.

The method was employed by Müller (1919), but it is one which requires a number of precautions which he did not clearly state. To avoid possible local changes in specific gravity the animals should be lightly narcotized, or perhaps killed by a mild electric shock. Attention should be paid to the shape of the body, contents of the gut, and such factors as the number of eggs or young. (The effects of gut contents and of young on the specific gravity of Cladocera have been described by Eyden (1923) and by Luntz (1929).) If it is necessary to raise the specific gravity of the water, the solute chosen for this purpose should preferably be non-toxic, have a low osmotic pressure, and a low rate of penetration through the skin of the animal. A high viscosity should also be avoided. During observations of specimens placed in this solution care should be taken to see that the specific gravity of the solution is correct, that it is evenly mixed, and that there are no disturbing currents. The specimens should be free from any liquid of a different density enclosed between limbs or clinging to other parts of the body. All the observations should be carried out as rapidly as possible so that interchanges between the body fluids and the solution may be reduced to a minimum.

The extent to which the forces of buoyancy and gravity may control orientation during swimming can be studied directly, if it is possible to allow the animal to swim in a solution of the type just described. The absence of any tendency to sink eliminates the possible influence of other methods of mechanical control, and most types of sensory mechanism can usually be excluded by suitable design of the experiment. Mechanical control by the forces of buoyancy and gravity, and perhaps some form of proprioception, then remain as the only possible explanations of any orientation which may occur. Good evidence in favor of the mechanical control would be secured if the animal swam in a position similar to that in which narcotized specimens had been found to float. Orientation by proprioception might still occur, but as will be shown later this remains at present as a rather doubtful possibility.

For animals whose specific gravity is equal to that of the water in which they live the only type of mechanical orientation possible is that which depends on the relative positions of the centers of gravity and buoyancy. In practice, however, it seems that a large number of free-swimming animals have a specific gravity somewhat above that of the water and that they persistently oppose the tendency to sink. Under these conditions other mechanisms can play their part and must, therefore, be considered in any study of mechanical orientation in the animals concerned.

To show whether or not the specific gravity is above that of the water, it is sufficient simply to watch an animal which has ceased to swim. To obtain a more quantitative value of the specific gravity a number of methods may be employed. That which has been used most frequently is based on the same floatation technique as has been just described. It is only necessary to know the specific gravity of the solution in which narcotized specimens of the animal will float without rising or sinking. The results obtained are usually not very accurate, although this may sometimes be due to neglect of the precautions listed above. Platt, however, (1899) gives figures for *Spirostomum* which appear to indicate an accuracy of about ± 0.001, and Luntz (1929) gives figures for rotifers which seem accurate to about ± 0.004. Ostwald (1903) has pointed out that the results will be least accurate when the viscosity of the medium and the surface resistance offered by the animal are unduly large. He suggests a modification of the method, by which he believes greater accuracy would be obtained. Instead of attempting to mix a solution in which the body will exactly float, he would prepare two solutions, in one of which the body would slowly rise, in the other of which it would slowly sink. The speeds of rising and sinking could be determined, and the specific gravity of the body would then be given by the formula, $S_k = \frac{G_1S_2 - G_2S_1}{G_1 - G_2}$, where S_k, S_1 and S_2 are the specific gravities of the body and of the two solutions, and where G_1 and G_2 are the speeds of sinking and rising which were observed. Ostwald assumes that in liquids of specific gravities equidistant above and below S_k, the rates of rise and fall would be equal. He states that this would actually be true, unless certain movable parts were extended during the motion in one direction, but were folded up during motion in the other. On this question, however, Ostwald has missed the essential point, namely that orientation of the body relative to the direction of motion must be made the same in each case. If this condition is not observed the fluid pressures met with during

rising and sinking will be different, except in the case of a body of identical form above and below. In practice this means that in all cases in which the centers of gravity and buoyancy do not coincide, the speeds of rise and fall must be fairly rapid, so as to ensure an orientation controlled entirely in the manner which has been illustrated in Fig. 6. This increases the difficulty, which was pointed out by Ostwald, of being certain as to whether or not a steady rate of motion has been attained.

Lowndes (1938a, b) has recently described a new method for determining specific gravity, which is apparently free from many of the objections associated with the previous methods. Titration of some substance added to the water affords a neat means of determining the actual volume of the animals, and the weight can then be found by a simple calculation involving this result and the results of weighing in specific gravity bottles. In a control test with small glass bubbles Lowndes found the results were accurate to about ± 0.002.

For large animals, such as fish, the weight can be determined in air, and the volume ascertained by direct measurement of the water displacement (Magnan, 1929). Or the weight may be determined both in air and in water, and the specific gravity then calculated from the formula, $\text{S.G.} = \frac{W_a}{W_a - W_w}$, where W_a and W_w represent the weights in air and water respectively (Tester, 1940). For small, spherical organisms, some use might be made of the well known method involving Stoke's law. Literature for various methods which have been used to determine the specific gravity of Protozoa is cited by Leontjew (1928).

From the point of view of animal orientation a determination of the specific gravity is not of fundamental importance, although it does permit a quantitative estimate to be made of the force which is required to prevent sinking. More important in this connection is a knowledge of the lines of action of the forces of propulsion and resistance. Unfortunately the methods which might be used to obtain this knowledge are not very satisfactory.

To determine the line of action of the propulsive force there seems to be little that can be done, other than to study the mode of action of the propulsive organs and the distribution of the currents which they create. Data secured in this way would indicate approximately the line of action of the propulsive force, but would not define its location with any great degree of accuracy.

Methods for observing the currents which surround a swimming animal usually depend on the addition of a suitable dye or of small particles to the water. The path and speed of such particles can be determined by appropriate methods of photography. An interesting technique which can be used to study some of the more definite currents, consists in adding to the water particles of tobacco mosaic virus, the observations being carried out through crossed polaroid plates which are placed on opposite sides of the vessel. The tiny, rod-shaped particles of the virus become orientated parallel to one another wherever there is a current, and they then possess the property of rotating plane polarised light, thus causing the currents to appear as bright streaks in an otherwise darker field (cf. Bawden *et al.*, 1936).

To determine the lines of action of the fluid resistance which is met with by a swimming animal is no less difficult than in the case of the propulsive force. Such methods of investigation as exist can mostly be applied only to dead or narcotized animals, and the results obtained may consequently have little direct application to the animals when alive.

It is relatively simple to determine the effects of fluid resistance on the orientation of the body when this is sinking passively in water. If the centers of gravity and buoyancy are known to coincide no experiment would be necessary, other than to observe the position in which the body sinks. If, however, the position which is then observed is one which might be caused by the tendency of the center of gravity to lie below the center of buoyancy, further tests have to be carried out. In a partcular example let us suppose that during passive sinking the same position is favored both by the fluid resistance and by the forces of gravity and buoyancy. This state of affairs could be demonstrated by transferring the narcotized specimen to fluids of greater density, adopting the precautions which have been outlined above. In a liquid in which the body very slowly rises, the orientation would remain the same as that seen during sinking. But in liquids of still higher density the rate of rising would increase, until finally the specimen would turn over because the effect of the fluid resistance had overcome that of the forces of buoyancy and gravity.

The essential features of this experiment were

recognized by Bethe (1894) and more recently by Müller (1919). It should be pointed out, however, that the forces of fluid resistance may favor a different orientation during passive sinking from that which they favor during constant forward locomotion. This is because in the former case the body is subjected to the downward pull of gravity alone, whereas in the latter case it is subjected to the net pull of gravity and propulsion. A body such as that shown in Fig. 4 would tend to lie on its side during passive sinking, although it would remain upright when exerting an active propulsive force. On the other hand a body constructed on the principle of the aeroplane might adopt the same orientation in both cases.

It is evident that the position in which the body of an animal will sink in water is not a safe guide to the position of stable equilibrium during active swimming. This statement requires some emphasis, in view of the fact that a surprising number of authors appear to have supposed that in order to determine the stable swimming position of

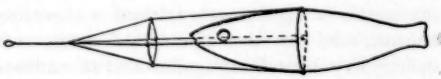


FIG. 9. ARRANGEMENT FOR TOWING THE BODY OF AN ANIMAL BY MEANS OF THREADS ATTACHED TO A GIRDLE NEAR THE CENTER OF GRAVITY

aquatic animals it is sufficient merely to observe the position in which dead or narcotized specimens will sink (Demoll, 1909; v. Buddenbrock, 1914; Herter, 1927; Langenbuch, 1928; Seifert, 1930, 1932; Oevermann, 1936; Foxon, 1936).

A different type of experiment, which might yield results of interest, would consist in towing the body of an animal through the water by means of a thread attached to a girdle near the center of gravity (Fig. 9). In some cases it might be found that if the body lay in its normal orientation it would start to rise when a certain speed of forward motion had been reached, attaining a level slightly higher than the point from which the thread was being pulled. A result of this kind would indicate the existence of "dynamic lift," at least at the particular angle of attack observed in the experiment. If the body displayed a definite tendency to maintain its normal orientation this would indicate some mechanism controlling rotations around the longitudinal axis. Care would be needed to have the pulling force act along a line as nearly as possible like that of the normal propulsive force, and it would be necessary to remember that the results might be different if the animal was alive and was surrounding itself with complex currents.

For a more precise study of the effects of fluid resistance on the inactive body of an animal it is desirable to use a wind tunnel, or a tank with flowing water if that can be arranged. The specimen, or an accurate model thereof, must be attached to some form of aerodynamic balance (cf. Harris, 1936). From the results obtained it should be possible to calculate the lines of action of the fluid resistance for a number of different angles of attack.

To study the effects of fluid resistance on the animal while alive and normally active, it would be necessary to devise some method by which the living animal could be attached in a current of water. Perhaps an attachment could be designed which would prevent the animal from moving forward and would keep it headed in one direction, but which at the same time would allow it freely to rotate around the antero-posterior axis, and would permit movements up or down or to either side. With an apparatus of this kind some interesting observations might be made, provided that there was no disturbance of the normal swimming movements.

As a preliminary experiment a captive animal could be placed in still water and if it was found able to rise up off the bottom, and to maintain itself at some intermediate depth, this might be regarded as evidence that the necessary lift was supplied by a vertical component of the propulsive force. The swimming movements, however, would be particularly liable to be disturbed, since the propulsive organs would have to work against a resistance of unaccustomed strength.

If the animal attached in this way proved unable to rise up off the bottom, it might be assumed that support was normally provided by "dynamic lift." This assumption could be tested for by introducing a current of water flowing antero-posteriorly past the animal, at about the speed usually attained during swimming. If the body was lying in its normal orientation the animal ought then to rise up and to remain at some higher level. A tendency to automatically assume and maintain the normal orientation would indicate some mechanism controlling rotations around the antero-posterior axis, and various tests might be

made in an effort to determine which this mechanism was. With an aerodynamic balance it might even be possible to work out lines of action of the fluid resistance.

The practical difficulties to be overcome in such experiments would be considerable, and the experiments are mentioned here only to indicate future possibilities. Always there would be the danger that the animal would attempt to escape from its attachment, or at least would carry out swimming movements which were not entirely normal.

A few other methods of experimentation are available in certain cases. Weights or air bubbles can be attached to the body of the living animal and the effect observed. Or parts of the body can be removed by operation. Thus Woltereck (1913) removed spines and other outgrowths of the body from various Cladocera, and then studied the effect of such operations on the swimming path. Sometimes results of value can be obtained by the use of an additional external force, such as that which is generated in a centrifuge. The work of Dembowski (1931) on the ciliate *Paramaecium*, affords an excellent idea of what may be done by intelligent use of this instrument.

THE POSSIBLE ROLE OF PROPRIOCEPTION

In an experiment which seeks to show the presence or absence of mechanical orientation in a free-swimming animal it is necessary to exclude, so far as possible, the several types of sensory orientation which might occur. It was unfortunate in the work of Bethe (1894, 1910) that he largely neglected the possible effects of light. At that time, however, it was generally believed that light could control only the antero-posterior orientation involved in "phototaxis." Rádl (1901) was the first to prove that light may also control a dorso-ventral orientation, and it was not until the work of v. Buddenbrock (1914) that this was shown to be a really widespread phenomenon. In experimental work it may not always be easy to exclude the occurrence of this type of orientation, especially since light is usually required for observation. But at least there need be no difficulty in devising control tests to show how far such orientation may be influencing a result.

Another type of sensory orientation is that in which statocysts are concerned. This it is usually possible to exclude either by damage to the receptor organs or by cutting through their nerve supply.

There will still remain, however, the possibility that the dorso-ventral orientation is controlled by some form of proprioception. At the present time our knowledge concerning the occurrence of this type of orientation is very incomplete. Experiments to prove its separate existence as distinct from purely mechanical orientation are not easy to design. But for this very reason there is perhaps a need for discussion of some of the factors involved.

Two main types of proprioceptive orientation would appear to be possible. In the first type the orientation would occur in response to pressure or tension, perceived in the skin, muscles, or elsewhere, and arising as a result of the support given to the body by a substratum or by the air or water. The size of the stimulus involved in such a mechanism would depend on the specific gravity of the animal in relation to its surrounding medium. In free-swimming aquatic animals the specific gravity is usually little or not at all above that of the water, so that the stimuli of the type just described are probably too weak to be of service for orientation. Breder and Harris (1935–6) have concluded on these grounds that proprioception most probably plays no part in the orientation of fish. Bethe (1894) went so far as to suppose that proprioceptive orientation can occur only in animals which rest on a solid substratum.

There is, however, a second possible type of proprioceptive orientation, which at least theoretically might occur, and which would not be influenced by the relative specific gravity of the external medium. The stimulus in this case would be caused by the direct action of gravity on freely movable internal organs or liquids, or on solids contained within these liquids. All such movable material would constantly tend to collect at the lowest possible point. This would create pressures and tensions which if perceived by the animal might serve as a basis for a more or less accurate sense of position. In man a proprioceptive sense of position undoubtedly exists, but it is not certain what types of proprioception are involved. Grahe (1926) takes the view that some part is played by each of the two main types distinguished here. James (1887) found that deaf and dumb people frequently lose all sense of position when submerged under water, a fact which suggests that only the first type of proprioception is concerned. The significance of James' experiments has been disputed, however, by Beck (1912).

It seems quite possible that proprioception of the second type may sometimes serve to contorl the orientation of certain fish. Rizzolo (1929) has shown that dogfish continue to swim in the normal position after total destruction of both the labyrinths, accompanied by transection of the olfactory tracts and of the optic nerves. The data given by Magnan (1929) indicate that these fish have a specific gravity only very slightly higher than that of sea water, and that they have the center of gravity placed a little above the center of buoyancy. These facts make it unlikely that the swimming position can be controlled by purely mechanical factors. Sensory control would thus appear to be involved, but the precise nature of this remains uncertain. It might be based on proprioception, or on a skin sensitivity to light, or on the perception of currents reflected from the sides and bottom of the aquarium.

V. Buddenbrock (1914, 1937) claims that proprioceptive orientation may be shown to exist in certain aquatic invertebrates. He suggests that this orientation occurs in response to movements of internal organs suspended in the body cavity. Experimental support for this idea was advanced by Wolf (1925), who found that in starfish a stimulus for orientation is provided by passive movements of the gut. Fraenkel (1928), however, claims to have disproved Wolf's results, and it would appear that proprioception of this type has not been proved to exist in any invertebrates. In particular nothing is known of the types of proprioception which perhaps occur in the species which are free-swimming.

Evidence that some type of proprioceptive orientation does occur in these forms is brought forward by v. Buddenbrock (1914). Most of his results, however, could be explained almost equally well on a purely mechanical basis. In one type of experiment v. Buddenbrock found that if the two crustaceans, *Leptomysis* and *Hemimysis*, were deprived of their statocysts and then placed in a horizontal beam of light, they swam vertically up and down, with their backs directed towards the light. The animals never swam horizontally, although their backs could have been turned towards the light in this position also. It was claimed that this result showed the existence of a proprioceptive sense of orientation. Another explanation, however, might be suggested. In order to swim horizontally with their backs towards the light the animals would have been compelled to lie on one side, a position which in many animals is mechanically more unstable than any other. The apparent choice of a vertical path may thus have been due to the fact that the animals were not able to orientate effectively to the light when they attempted to swim horizontally.

In another experiment v. Buddenbrock found that if *Hemimysis* was kept in bright sunlight and then suddenly transferred into red light, the animals continued to swim in the normal position, although both the statocysts had been removed. It was assumed that the light-adapted animals were not able to perceive the red light and that the position in which they swam was mechanically unstable. These assumptions, however, were not supported by experimental evidence. With *Palaemon* v. Buddenbrock found that adult individuals from which the statocysts had been removed would often persistently swim with the back directed upwards, even when illuminated only from below. The position adopted was again supposed to be mechanically unstable, but no attempt was made to offer experimental proof.

Perhaps the most convincing experiments which favor the idea of proprioceptive orientation in a free-swimming form, were those of Demoll (1909) on the crustacean, *Squilla*. Demoll found that blinded individuals of this animal persistently swam with the back directed upwards, even when the back was weighted by small pieces of lead which were over one fifth the total weight of the body. It was especially noted that the animals soon turned upside down whenever the swimming movements became less energetic. This makes it clear that a tendency for the center of gravity to lie below the center of buoyancy could not have been responsible for the animal's continued ability to maintain the normal position. Some other mechanism might have been concerned, in which the magnitude of the force of propulsion or resistance played an essential part (for example a mechanism such as that illustrated in Fig. 4), but this appears most unlikely. Demoll assumed that the blinded animals would not be able to orientate to light, and in this he probably was correct. Nevertheless dorso-ventral orientation to light may sometimes be controlled by photosensitivity of the skin, as for example in the leech (Schlüter, 1933) and perhaps in certain beetle larvae (Wojtusiak, 1929). This might also be true for *Squilla*, though v. Buddenbrock (1914) found that unblinded adult animals did not always turn upside down when

the light was placed below, so that the reflex orientation to light is not especially well developed. The possibility remains that the orientation is controlled by statocysts, as was supposed by Demoll. But no such organs have yet been found in *Squilla*, and v. Buddenbrock argues on physiological grounds that they probably do not occur.

Recently the view that proprioceptive orientation may occur in free-swimming animals has been supported by Oevermann (1936), who worked with aquatic Hemiptera. He claimed that when these animals are in need of air they still are able to find the water surface, even after being blinded and deprived of their antennae, after having the abdominal nerve cord cut through, and with the body weighted so that the usual swimming position has become unstable. He also maintained that the animals will attempt to preserve the normal swimming position, even when this has been rendered unstable by the attachment of weights or by the removal of air from the surface of the body. These experiments are of great interest, but unfortunately Oevermann's descriptions are not always sufficiently objective, and no experimental evidence was given concerning the alleged stability or otherwise of the different swimming positions which he observed.

If proprioceptive orientation should be shown to be absent in a free-swimming animal, this would not necessarily mean the absence of proprioception. Bethe (1894) denied that a purely proprioceptive orientation could occur in swimming or flying animals. Yet he maintained that if mechanical forces favored one position the animal would always know the angle at which it lay in relation to this position, simply by the feeling in the muscles. It is possible that Bethe believed that the amount of mechanical torque within the body could be perceived directly, although this seems most unlikely. More probable would be some form of proprioception within such various steering organs as are required to deflect the animal from the stable orientation.

Sensory control of the swimming position might also be based on a surface sensitivity to currents. In animals with a specific gravity above that of the surrounding water there would be a tendency to sink whenever the normal swimming position is temporarily lost. At such times the pattern of currents around the body would be changed, and if the animal could perceive these changes reflex righting movements might occur. Alverdes (1927) has suggested a sensory mechanism of somewhat this type for larvae of the insect *Cloeon*.

Close to the bottom or to the surface of the water some reflex orientation might occur through the perception of "echo currents." Townsend (1939) has reported a sensory perception of this kind in the heteronereis stage of a species of polychaete worm, and a similar function can be ascribed to the lateral line organs of certain fish (Dykgraaf, 1934).

DISCUSSION

The orientation of a typical free-swimming animal involves rotations around three major axes, longitudinal, dorso-ventral, and transverse. There are, however, two main types of orientation, of which that discussed in the present paper can be described as "dorso-ventral" and involves rotations around only the transverse and longitudinal axes. Control of these rotations may be purely mechanical or it may be reflex and sensory. The situation is complicated because several types of control may act together, or there may be various factors which are opposed to each other. Investigations of dorso-ventral orientation must therefore deal with all these different factors, and an experiment which takes into account only the sensory or only the mechanical factors, may easily lead to a false result.

The second of the two main types of orientation is that which is involved in the familiar "phototaxis" and in various other forms of "taxis." Orientation of this kind may be described as "antero-posterior" and is associated with rotations around the transverse and dorso-ventral axes. The control of rotations around the latter axis must be always sensory, unless the animal lies on one side, but control of the rotations around the transverse axis may be either sensory or mechanical. This means in practice that, if an experiment on any form of taxis is concerned with turns up or down, then mechanical as well as sensory factors must be given full consideration.

Mechanical factors very similar to those involved in orientation are also of great importance in the problems connected with floatation (reviewed by Jacobs, 1935) and with cyclomorphosis (reviewed for *Daphnia* by Coker, 1939). The earlier workers in these fields were often inclined to exaggerate some one particular feature, while they overlooked the important relations which may exist between the shape of the body and the

pattern of surrounding fluid pressure. Thus Wesenberg-Lund (1908) was of the opinion that the spines and other outgrowths of planktonic organisms are of special importance because they shift the position of the center of gravity. It was the brilliant work of Woltereck (1913) which first clearly showed that such organs may play a significant rôle in controlling the orientation of the body relative to its line of motion, by virtue of the resistance which they offer to movement through the water.

SUMMARY

1. Most aquatic animals swim in some typical position which bears a definite relation to the axes of the earth. Control of this position may be either sensory or mechanical.

2. A standard swimming position may have certain mechanical and ecological advantages for the animal.

3. The most important type of mechanical orientation is probably that in which the center of gravity tends to lie below the center of buoyancy. Other mechanisms may exist which involve the lines of action of the forces of propulsion and resistance, but such mechanisms can occur only when the specific gravity of the animal exceeds (or is less than) that of the water. If there is a tendency to sink which is resisted by a vertical component of the propulsive force the animal will perhaps swim in jumps, allowing its body to be orientated by fluid pressures during the brief periods of passive sinking. When support is provided by a vertical component of the resistance the animal may be orientated by a mechanism similar to that found in aeroplanes.

4. The various types of mechanism could be combined together in almost any way. Changes in shape shown by the swimming animal, and currents created by its own activity, may provide further complications.

5. There are a few practical methods which can be used for the study of mechanical orientation in aquatic animals, but many of the problems cannot be solved by methods known at present. Care is always required to eliminate sensory factors, and so far as possible to study the different mechanical factors isolated from each other.

6. Sensory reflex control of the swimming position may depend on a response to light, or on a response to gravity perceived by statocysts. If proprioception sometimes plays a part, the stimulus would probably be provided by the downward pressure of freely movable internal organs or liquids. Occasionally a surface sensitivity to currents could serve to control the orientation during downward sinking, or in response to "echo currents."

7. A knowledge of the mechanical factors which may control dorso-ventral orientation can also be of importance in the study of antero-posterior orientation ("taxes") and of such subjects as floatation and cyclomorphosis.

The writer is much indebted to various persons who have offered valuable criticisms and suggestions. In particular he wishes to thank Professor S. O. Mast, Professor J. C. Hubbard and Dr. C. F. Bonilla, all of the Johns Hopkins University.

LIST OF LITERATURE

ALVERDES, F. 1927. Die Raumorientierung der Cloëon-Larve. *Z. vergl. Physiol.*, 5: 598–606.

BAWDEN, F. C., N. W. PIRIE, J. D. BERNAL, and I. FANKUCHEN. 1936. Liquid crystalline substances from virus-infected plants. *Nature, London*, 138: 1051–52.

BECK, K. 1912. Untersuchungen über den statischen Apparat von Gesunden und Taubstummen. *Z. Sinnesphysiol.*, 46: 362–78.

BETHE, A. 1894. Ueber die Erhaltung des Gleichgewichts schwimmender Tiere. *Biol. Zbl.*, 14: 95–114 and 563–82.

——. 1895. Die Otocyste von *Mysis*. Bau, Innervation, Entwicklung und physiologische Bedeutung. *Zool. Jahrb.* (*Anat.*), 8: 544–64.

——. 1910. Notizen über die Erhaltung des Körpergleichgewichts schwimmender Tiere. *Festschr. R. Hertwig*, 3: 81–92.

BORELLI, G. A. 1681. De Motu Animalium. *Rome.* (For German translation of part on flight and swimming see Ostwald's "Klassiker der exakten Wissenschaften," Nr. 221. 1927).

BREDER, C. M., JR., and J. E. HARRIS. 1935–6. Effect of light on orientation and stability of young plectognath fish. *Carnegie Inst. Wash. Publ.* 452. *Papers Tortugas Lab.*, 29: 23–36.

v. BUDDENBROCK, W. 1914. Über die Orientierung der Krebse im Raum. *Zool. Jahrb.* (*allg. Zool.*), 34: 479–514.

——. 1937. Grundriss der vergleichenden Physiologie. 2. Aufl., Bd. I. Borntraeger, *Berlin.*

COKER, R. E. 1939. The problem of cyclomorphosis in *Daphnia*. QUART. REV. BIOL., 14: 137–48.

DEMBOWSKI, J. 1929. Die Vertikalbewegungen von *Paramaecium caudatum*. I. Die Lage des Gleich-

gewichtscentrums im Körper des Infusors. *Arch. Protistenk.*, 66: 104–32.

——. 1931. Die Vertikalbewegungen von *Paramaecium caudatum*. III. Polemisches und Experimentalles. *Arch. Protistenk.*, 74: 153–87.

DEMOLL, R. 1909. Über die Augen und die Augenstielreflexe von *Squilla mantis*. *Zool. Jahrb.* (*Anat.*), 27: 171–212.

DYKGRAAF, S. 1933–4. Untersuchungen über die Funktion der Seitenorgane an Fischen. *Z. vergl. Physiol.*, 20: 162–214.

EYDEN, DORA. 1923. Specific gravity as a factor in the vertical distribution of plankton. *Proc. Camb. Philos. Soc.* (*Biol. Sci.*) [contin. as *Biol. Rev.*], 1: 49–55.

FOXON, G. E. H. 1936. Orientation of *Chirocephalus* and *Daphnia*. *Nature, London*, 137: 948–49.

FRAENKEL, G. 1928. Über den Auslösungsreiz des Umdrehreflexes bei Seesternen und Schlangensternen. *Z. vergl. Physiol.*, 7: 365–78.

GRAHE, K. 1926. Die Funktion des Bogengangsapparates und der Statolithen beim Menschen. *Hdb. norm. path. Physiol.*, 11: 909–84.

HARRIS, J. E. 1936. The rôle of the fins in the equilibrium of the swimming fish. I. Wind-tunnel tests on a model of *Mustelus canis* (Mitchill). *J. Exp. Biol.*, 13: 476–93.

——. 1937. The mechanical significance of the position and movements of the paired fins in the Teleostei. *Carnegie Inst. Wash. Publ.* 475. *Papers Tortugas Lab.*, 31: 171–89.

——. 1938. The rôle of the fins in the equilibrium of the swimming fish. II. The rôle of the pelvic fins. *J. Exp. Biol.*, 15: 32–47.

HERTER, K. 1927. Reizphysiologische Untersuchungen an der Karpfenlaus (*Argulus foliaceus*). *Z. vergl. Physiol.*, 5: 283–370.

JACOBS, W. 1935. Das Schweben der Wasserorganismen. *Ergebn. Biol.*, 11: 131–218.

JAMES, W. 1887. The sense of dizziness in deaf mutes. *Amer. J. Otology*, 4: 239– [Cited from Nagel, *Hdb. Physiol. Menschen*, 3. Vieweg, Braunschweig. 1905.]

LAMB, H. 1924. Hydrodynamics. Fifth Edition. Univ. Press, *Cambridge*.

LANGENBUCH, R. 1928. Über die Statocysten einiger Crustaceen ... etc. *Zool. Jahrb.* (*allg. Zool.*), 44: 575–622.

LEONTJEW, H. 1928. Zur Biophysik der niederen Organismen. IV. Mitteilung: die Bestimmung des spezifischen Gewichts der Plasmodien und Sporen bei den Myxomyceten. *Z. vergl. Physiol.*, 7: 195–200.

LOWNDES, A. G. 1937. Body orientation in Crustacea. *Nature, London*, 140: 241–42.

——. 1938a. Density of living aquatic organisms. *Nature, London*, 141: 289–90.

——. 1938b. The density of some living aquatic organisms. *Proc. Linn. Soc. London*, 150: 62–73.

LUNTZ, A. 1929. Weitere Untersuchungen über die Sinkgeschwindigkeit von Süsswasserorganismen. *Zool. Jahrb.* (*allg. Zool.*), 46: 465–82.

MAGNAN, A. 1929. Les caractéristiques géometriques et physiques des poissons, avec contribution á l'étude de leur équilibre statique et dynamique. *Ann. Sci. nat.* (*Zool.*), (10), 12: 5–136.

——. 1930. Same title. *Ann. Sci. nat.* (*Zool.*), (10), 13: 355–489.

MAGNUS, R., and A. DE KLEIJN. 1930. Körperstellung, Gleichgewicht und Bewegung bei Säugern. *Hdb. norm. path. Physiol.*, 15, 1: 29–54.

v. MISES, R. 1936. Fluglehre. Vorträge über Theorie und Berechnung der Flugzeuge in elementarer Darstellung. 5. Aufl. Springer, *Berlin*.

MÜLLER, R. T. 1918–19. Tanymastix lacunae (Guérin) aus dem Eichener See (südl. Schwarzwald. *Z. Biol.*, 69: 141–274.

OEVERMANN, H. 1936. Das statische Verhalten einiger Wasserwanzenarten. *Z. wiss. Zool.*, 147: 595–628.

OSTWALD, W. 1903. Zur Theorie der Schwebevorgänge sowie der specifischen Gewichtsbestimmung schwebender Organismen. *Arch. gesamt. Physiol.*, 94: 251–72.

PARKER, G. H. 1922. The geotropism of the sea-urchin *Centrechinus*. *Biol. Bull.*, 43: 374–83.

PARR, A. E. 1927. Keeling sick fishes. *Bull. New York Zool. Soc.*, 30: 66–67.

PLATE, L. 1924. Allgemeine Zoologie und Abstammungslehre. Zweiter Teil: Die Sinnesorgane der Tiere. Fischer, *Jena*.

PLATT, JULIA B. 1899. On the specific gravity of *Spirostomum*, *Paramaecium*, and the tadpole in relation to the problem of geotaxis. *Amer. Nat.*, 33: 31–38.

RÁDL, E. 1901. Über den Phototropismus einiger Arthropoden. *Biol. Zbl.*, 21: 75–86.

RIZZOLO, A. 1929. A study of equilibrium in the smooth dogfish—*Galeus canis* (Mitchill). *Biol. Bull.*, 56: 383–89.

SCHLÜTER, C. 1933. Die Bedeutung des Centralnervensystems von *Hirudo medicinalis* für Locomotion und Raumorientierung. *Z. wiss. Zool.*, 143: 538–93.

SEIFERT, R. 1930. Sinnesphysiologische Untersuchungen am Kiemenfuss (*Triops cancriformis* Bosc.). *Z. vergl. Physiol.*, 11: 386–436.

——. 1932. Raumorientierung und Phototaxis der Anostraken Euphyllopoden. (Versuche an *Chirocephalus* und *Artemia*.). *Z. vergl. Physiol.*, 16: 111–84.

TESTER, A. L. 1940. A specific gravity method for determining fatness (condition) in herring (*Clupea pallasii*). *J. Fish. Res. Board Canada* (formerly *Biol. Board*), 4, 461–71.

TOWNSEND, GRACE. 1939. A vibration sense in a swarming annelid. [Abstract]. *Biol. Bull.*, 77: 313.

WESENBERG-LUND, C. 1908. Plankton-Investigations of the Danish Lakes. II. *Kopenhagen.*

WILLIAMS, S. R. 1900. The specific gravity of some fresh-water animals in relation to their habits, development, and composition. *Amer. Nat.*, 34: 95–108.

WOJTUSIAK, R. J. 1929. Über Lichtreaktionen normaler und geblendeter Acilius-Larven. *Acta Biol. exp. Warszawa*, 3: 165–74. [Cited from *Ber. wiss. Biol.*, 12: 684. 1929.]

WOLF, E. 1925–6. Physiologische Untersuchungen über das Umdrehen der Seesterne und Schlangensterne. *Z. vergl. Pyysiol.*, 3: 209–24.

WOLTERECK, R. 1913. Über Funktion, Herkunft und Entstehungsursachen der sogen. "Schwebe-Fortsätze" pelagischer Cladoceren . . . etc. *Zoologica, Stuttgart*, 26: 475–550.

THE PITUITARY BODY IN GIANT ANIMALS FOSSIL AND LIVING: A SURVEY AND A SUGGESTION

By TILLY EDINGER

Palaeontological Department, Museum of Comparative Zoology, Harvard College, Cambridge, Massachusetts

WHEN G. Elliott Smith, comparative anatomist of the brain, in his description of an endocast of the cranial cavity of a giant Moa briefly remarked "The hypophysis is very large" (1902), little was yet known of the relation of the pituitary gland to body size. Nor could F. Nopcsa, the palaeozoologist, realize the full implications when he demonstrated that the fossa hypophyseos is larger, in relation to the brain cavity proper, in giant dinosaurs than in their smaller relatives (1917). For the definite proof of the influence of the pituitary gland on body growth, the separation, from the many other substances produced by the gland, of the anterior lobe growth hormone, was not achieved until 1921 (H. M. Evans).

I. PITUITARY GLAND AND BODY SIZE: SOME ESTABLISHED FACTS

Pathology

The normal growth-regulating function of the pituitary body (PB) was first inferred from its disturbances in man. Human growth disturbances were found to be accompanied by abnormal PBs: dwarfs suffer from hypopituitarism, abnormally tall men from hyperpituitarism. The latter disease occurs in two forms. In acromegaly, the sella turcica of the sphenoid bone is enlarged (in 93 per cent of cases) by a tumor in which the acidophilic secretory cells of the anterior pituitary lobe are increased. In human giantism, in contrast to acromegaly, intensive growth starting before or during adolescence produces a well-proportioned abnormally tall skeleton; hyperplastic changes in the anterior pituitary lobe widen, lengthen, and deepen the sella.

While we know that size variations occurring normally in nature tend to "mendel back" to medium size (unless selected by breeders), clinicians have found family predisposition to pituitary diseases; for example, three sisters and a brother described by J. Bauer were normally built giants of 190, 185 and 183 cm. in height and an achondroplastic dwarf of 121 cm. Geneticists also have ascertained a linkage between defective development of the animal PB and the inheritance of structural distortions (Stockard, in *The Pituitary Gland*, cf. Bibliography).

Experiments

Animal experiments have shown that, when the pituitary body is removed, growth stops altogether and cannot be revived by any kind of medication, whereas the slowing down of growth in thyroidectomized animals is entirely cured by treatment with anterior lobe extracts (Evans, in *The Pituitary Gland*). Natural dwarfs occurring in Evans' rat colony were always restored to complete normality by administration of the growth hormone (Evans *et al.*, '33).

In the normal rat, the response of the bones to injections of anterior lobe extract is an overstimulation of normal periosteal growth (cf. for example, Evans, Handelsman). Injected rats become twice as heavy as the controls; some of them surpass the normal maximum size of the species. The absence of acromegalic stigmata in these giant rats has been attributed to the fact that in rats the bone epiphyses never unite (Putnam, in *The Pituitary Gland*). This assumption is based on the disputed doctrine that giantism is the acromegaly of youth. Experiments with various breeds of dogs tend to show (if conclusions

may be drawn from the reaction of so few individuals) that racial constitution decides the result of experimental hyperpituitarism. An English bulldog grew to almost twice the weight of littermate controls through anterior lobe injections; growth, however, was not evenly distributed but typically acromegalic (Putnam *et al.*). In dachshunds, symmetrical overgrowth = giantism occurred consequent on injections, the only outstanding acromegalic feature being folded skin (Evans *et al.*). In sheep-dogs likewise, no difference of the skeletons was observed, apart from size, between an experimental giant of 30 kg. and its litter control of 20 kg. weight (Evans *et al.*).

Hypophysectomized chick embryos never reached the size of controls of the same age (Fugo). As far as the writer is aware, none of the records of pituitary injection experiments on birds, nor any report on reptile experiments mention the animals' size. In the case of the sauropsids, therefore, palaeontological data (see below) fill an actual gap in the chain of proofs of the rôle played by the PB in conditioning body-size—already decisive enough, however. A diet of cattle anterior lobe not only increased the rate of growth in *Amblystoma*, but these newts never ceased to grow after reaching the normal maximum size of the two species used in Uhlenhuth's experiments.

Relative size of the pituitary body

In endogenous giants, the size of the PB was stated above to vary in direct proportion to the amount of secretion. This applies not only to human pathological cases but may become apparent in normal size variation. In the larger breeds of cattle, and in the larger individuals within a breed, the PB is larger in relation to body size than in smaller ones (Petersilie). A moderate positive correlation exists between the weight of the PB, but particularly of the anterior lobe, and body size in the normal adult human (Rasmussen, in *The Pituitary Gland*). Large human skulls have in general larger sellae turcicae than small skulls (Kadanoff). In the exogenously developed experimental giants the PB is, of course, not, or hardly, enlarged, supply from outside replacing hypersecretion. The foxhound bitch injected by Benedict *et al.* grew to 150 percent the weight of its sister, yet the increase in PB weight was only 7 percent; uterus and ovaries were 300 percent, thyroid and spleen, 100 percent heavier; the difference in brain weight amounted to no more than 3 percent.

We are here facing a phenomenon which has an extremely important bearing on our present investigation: the fact that brain growth follows other laws than body growth and PB growth.

Experimental proofs thereof are abundant. Mortimer, investigating only the skulls of young rats after hypophysectomy, observed that snout growth is more impeded than the development of the brain case, and that post-operative treatment with growth hormone produces satisfactory growth only in the snout. In the giant rats produced by the experiments of Rubinstein (in *The Pituitary Gland*), the brain was always smaller in relation to body size than in normal rats. Rubinstein's extensive experimental and mathematical investigation definitely showed that the growth hormone, while markedly stimulating body growth, fails to affect the growth or structure of the central nervous system.

The palaeontological aspect

This only confirms the palaeozoologists' experience of phylogenetic increase in body size. The comparative anatomist too is, of course, well aware that the brain and neurocranium of a larger animal are smaller in relation to body size than those of its smaller congener. The palaeontologist sees the neurocranium actually lagging behind during phylogenetic increase of body size, as a rule, and always in the evolution of definite giants.

The recent achievements of medicine and experimental zoology now reveal the seat of the force which must have promoted phylogenetic body growth as it does ontogenetic growth. They enable the palaeontologist to investigate, as directly as is possible within his realm, the growth organ itself, and to check the development of its size—that is, its power—with that of the brain even where only skulls are preserved.

Due to its complex origin, the pituitary, master among endocrine glands, is, so to speak, directly accessible to palaeo-anatomical investigation. The PB is lodged in the brain case because its "posterior lobe" (posterior in man) is its pars nervosa, the neurophysis, ontogenetically a downward diverticulum from the floor of the diencephalon. Yet it lies below the brain case proper and may be provided with its own capsule by the sphenoid bone (the sella turcica in man), because its epithelial portion, the hypophysis s. str. ("anterior lobe" = pars glandularis, etc.) is a pars buccalis, ontogenetically the terminal part of an upward

diverticulum from the dorsal side of the roof of the mouth.

Until now, however, apart from dinosaur giantism only one phylogenetic trend has been interpreted in terms of hyperpituitarism: Keith found that the differences between *Homo sapiens* and *Homo primigenius* are mainly the latter's acromegalic symptoms! This view had also been taken by Larger, but he emphatically denies the connection between PB and *l'acromégalie-gigantisme*. In vain the palaeozoologist searches neozoological literature for data of animal PBs with reference to the formation of their specific body size (except for the papers of Robb and Rost discussed below); nor have any investigators of animal and human PBs taken into account the palaeozoological facts referred to in our introductory sentences. Yet normal animals, living and extinct, testify plainly to the phylogenetic significance of the pathological, statistical, and experimental observations which may be summarized as follows:

(1) Body-growth, but apparently not brain growth, is dependent upon the amount of growth hormone produced by the anterior lobe of the PB. (2) More hormone is produced by large glands than by small ones. (3) Hyperpituitarism enlarges the sella turcica. (4) Tendency to hypo- and hyper-pituitarism is hereditary. (5) Hyperpituitarism can produce animals above maximum normal size.

II. REPTILES

[No Anamnia have been studied with regard to our subject. Enlightening differences might be revealed by comparisons of the PB of giant fish with that of smaller congeners such as a 450 kg. *Thunnus* and an 8 kg. *Neothunnus*. Likewise, there doubtless exist differences between the PB of small frogs and that of the 30 cm.-long *Rana goliath*; in Herrick's figures of the middle sections of brains of adult *Amblystoma tigrinum* (maximum body size 27 cm.) and *Cryptobranchus alleghaniensis* (55 cm.), I find the glandular lobe of the PB less than half as long as the tectum mesencephali in the smaller but exactly as long as the tectum in the larger newt.]

There are giants among the living reptiles such as 5 m.-long snakes, 2 m.-long turtles, and 3 m.-long lizards; their PBs remain to be studied, and to be compared with those of the small representatives of these orders. The size of lizard PBs should, furthermore, be compared with the volume of the pituitary fossa of 8–10 m.-long mosasaurs: this pouch in the skull base was the bony capsule of the PB and thus reproduces approximately the size of the long-vanished gland. Some reptiles, however, are excluded from palaeoendocrinological investigation by the fact that only the distal extremity of their PB lies in no more than a trough-like depression on the sphenoid bone. In others, the fossa may retain its embryonic condition, that is, remain open across the entire sphenoid bone. Thus, the ichthyosaurs should prove particularly favorable objects for comparative investigation. It appears that this could be undertaken on intact skulls. A widely open cranio-pharyngeal canal penetrates the basisphenoid of some ichthyosaurs. Endocasts of this canal might exhibit illuminating differences between specimens of different size; the outside opening has been found in the largest known (2 m.-long) *Ichthyosaurus* skull as well as in smaller specimens. The pituitary space proper is a well-marked expansion within the cranio-pharyngeal canal of the giant dinosaur family Atlantosauridae of which it is believed that this persistent communication between the brain and mouth cavities was a family character. (O. C. Marsh: for literature on fossil brain cavities see lists in Edinger, 1929 and 1937.)

It is, of course, no mere coincidence that the only animals so far described as having, so to speak, disproportionately large pituitary fossae are the giants par excellence—the dinosaurs. In Jurassic sauropod skulls, the 25 m.-long but slimly built *Diplodocus* shows a slender sac below the brain case as deep as this is high; in the stouter 17 m.-long *Camarasaurus*, the lower part of the sac has a much greater diameter than the upper (Fig. 1): the "anterior lobe" of the PB being ventral to the other parts in reptiles. Apart from the fossae of giant sauropods which he briefly characterized as *ungeheuer* (monstrously large), Nopcsa investigated the fossae of seven small and seven large dinosaur genera. This enabled him to restrict direct comparison to genera of established ancestry. His interpretation of *dinosaur giantism as being the result of an increase in pituitary function* is therefore based on the, so to speak, actual observation of a process, namely that "bei diesen Tieren im grossen und ganzen mit der Zunahme der Körpergrösse eine Zunahme der Hypophyse ihrem Hirn gegenüber Hand in Hand geht . . . die Grösse des Hirnschädels bleibt dabei stationär." This means that, in dinosaurs, phylogenetic increase in body-size was accompanied by

an increase in size of the PB, while brain size remained the same. The many endocranial casts of dinosaurs now known prove the basic truth of Nopcsa's ('17) doctrine.

Brown and Schlaikjer note among the differences between the endocranial cast of the primitive small ceratopsian *Protoceratops* from the Mongolian Upper Cretaceous and that of the large advanced *Anchiceratops* from the American Upper Cretaceous ('40, p. 192) that the PB in the former is "relatively small and narrow," in the latter, "relatively large and broad." Dr. Brown very kindly allowed the present writer to examine the

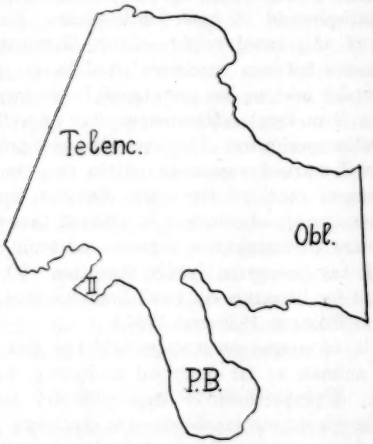


FIG. 1. OUTLINE OF ENDOCAST OF BRAIN CAVITY OF CAMARASAURUS SUPREMUS

From left side, after Osborn. Two-fifths natural size. Telenc.: cast of caudal portion of forebrain chamber. Obl.: cast of medulla oblongata chamber. II: cast of optic nerve canal. PB: cast of fossa pituitaria.

two endocasts. The length of the brain case, from the notch between the olfactory and optic nerve foramina to the foramen magnum, was found to be 65 mm. in *Protoceratops* and 72 mm. in *Anchiceratops*. Brain length, however, measured from that notch to the posterior end of the cerebellum, was exactly the same in the small and the large forms, viz., 49 mm.: only the medulla oblongata was more voluminous in the giant. The *Protoceratops* skull from which the cast was taken is 611 mm. long. The only complete *Anchiceratops* skull is 1660 mm. long but is from a smaller individual than that which furnished the cast (Sternberg). On the other hand, the difference between the casts of the pituitary fossae is indeed very striking. Both are well set off from the brain cast proper by a stalk. Their greatest lengths, breadths and heights are: *Protoceratops*, 13, 11, 21 mm.; *Anchiceratops*, 14, 21, 37 mm. While in *Protoceratops* the pituitary fossa tapers in breadth and length and its cast is a pointed wedge, that of *Anchiceratops* retains the same breadth and length almost to the lower extremity.

Exact data on the relative sizes of brain case and pituitary fossa in dinosaurs have been given by Janensch ('35)—data which are not known of any living animal. Janensch was able to study several brain casts of three Jurassic sauropod genera, the entire skeletons of each of which were known to him and, in one instance, even that of the very individual which furnished a cast. This was a representative of those greatest giants which ever trod the earth, viz. the genus *Brachiosaurus* which could raise its head 12 m. above the ground; the body reached 25 m. in length, and some 50 tons in weight.

Janensch estimates the body of his specimen in life at 25 cubic meters. It has a brain cavity proper of 309.5 cubic cm. and a fossa hypophyseos 13.8 ccm. = 4.5 percent of the brain cavity. In a smaller *Brachiosaurus* skull, the proportion is 198.2:15.2 = 7.4 percent. In the smaller genus *Barosaurus*, in an individual the body of which was estimated at 15 cubic meters, a brain cast of 198.8 ccm. had a much larger hypophyseal appendage—18.5 ccm. = 9.4 percent. Within the species, however, the smaller the skull, the smaller the relative size of the PB was found to be—for instance, 9.2 ccm. = 7.6 percent of the 120.8 ccm. brain cavity. In the still smaller *Dicraeosaurus* (skeleton-length 13.20 m.), the numbers, including a parietal sinus of the brain cavity, are 194:14 = 7.2 percent; excluding the sinus, 140.8: 14 = 9.9 percent.

These figures prove that there existed a tribe of animals in which the PB was so large that the volume of its capsule was as much as $\frac{1}{10}$ of the brain case volume. This was the group which contained the largest terrestrial animals ever known.

Pointing to the prevalent sterility in human giants and acromegals, Nopcsa suggested that hyperpituitary decrease of sex functions, along with the general decrease of natural resistance in any giant body, was the cause of *extinction* of the sauropods. In our opinion, Nopcsa goes too far in stressing the parallel between

the normal dinosaur giantism and the human hyperpituitary diseases. Particular objections spring from two standpoints:

1. The sauropods flourished for many millions of years after reaching giant size. Abundant up to the end of the Cretaceous period, they then disappeared together with practically all characteristically Mesozoic phyla, small and big.

2. The anterior pituitary lobe itself also produces a sex hormone, and this normally prevails over the growth hormone in the adult. Sexual dysfunction in hyperpituitary women has been observed by Henderson to occur only when the sella turcica is considerably enlarged by an adenoma of the PB. This pathological growth compresses the cells which elaborate the hormones controlling sex function, but it does not destroy them. After operations with radical extirpation of the adenoma, Henderson found that the normal menstrual cycle was resumed and pregnancy occurred. The enlargement of the dinosaur fossa hypophyseos, however, was normal. Animal experiments too have shown that certainly not every kind of hyperpituitarism causes sterility. Experimental administration of cattle anterior lobe, even though disturbing the sexual rhythm in young rats, has increased sex activity in senile rats, caused hens to lay more and larger eggs, produced hypertrophy of the gonads in young alligators, and stimulated the ovaries of frogs.

III. BIRDS

The general remark in the *Handbuch der Zoologie* on the avian PB, *"wenig entwickelt"* (Stresemann, p. 107), calls for correction. Küenzi's comparisons of the brain-part surfaces throughout the bird system showed that the PB is relatively small, for instance, in sparrows, rather large in fowl, and very large in the ratites.

The greatest body-size also is attained by the earth-bound ratites. The largest ostriches reach 260 cm. body-height; the largest flying bird, the albatross, 116 cm.

Flightless types in various euornithid orders also developed giant forms. The largest living penguin, the emperor, stands 1 m. high. Its PB should be investigated together with that of a small penguin. A Miocene penguin was twice as large as the emperor penguin. Its skull, however, is still unknown, and so is the skull of an Eocene ground-bird of fourfold ostrich-height.

The largest ratite genera are also extinct. Complete skeletons have been mounted from medium-sized bones only, not from the largest. That of a *Dinornis maximus*, the New-Zealand Moa, is 255 cm. high; one of the Madagascar *Aepyornis maximus*, 300 cm.

Now the very strata which contain the remains of these subfossil heavy giants have also furnished remains of smaller, lighter-built representatives of the respective families to which the giants belong, down to the size of a turkey. It is obvious that the smaller forms, although they lived together with the giants, are less advanced types. They are therefore considered the ancestral forms (Lambrecht), and we here possess evidence of *development of giantism within families*. Since the avian brain is so tightly fitted into the skull that endocasts furnish exact replicas of the brain form, and since the avian PB, set well off the brain by its long stalk, is encased in a separate bony chamber, the two ratite families furnish excellent tests of the problem we are concerned with.

Dinornithids

We have said that Elliot Smith was struck by the size of the PB in the Moa. Owen, too, who first described the brain of *Dinornis maximus*, had remarked in 1872: "The hypophysis, as represented by the cast of the sella, is of considerable size." The significance of this becomes apparent when the *Dinornis* endocast (Royal College of Surgeons, London, catalogue number D. 148) is compared with an endocast of the smaller dinornithid *Anomalapteryx* (Senckenberg Museum, Frankfurt a.M., Av. 29 a).

Not having sawed skulls at hand in which to measure the interior spaces, and not being able to take volumetric measurements on the plaster casts or to apply a formula to those differently shaped parts of the casts, the writer took recourse to a simple method feasible for comparison, though inaccurate as to absolute size. The three diameters of the PB casts were multiplied with each other, and so were those of the forebrain casts (the form of which, unlike that of other brain parts, is similar in both families investigated). The imaginary cubes, of course, suggest volumes larger than are actually present either in the wedge-shaped or globular PBs or the heart-shaped forebrains. As, however, they are only computed for the sake of comparison with each other, the relative figures at which we are finally aiming, the proportion of the cubes, cannot be far from the true proportions of PB and forebrain. Indeed, Rost calculated the volume of the PB in two races of pigeon by addition of section superficies as well as by multiplication of the diameters of the PB and, in spite of the difference in the resulting absolute numbers,

found practically the same inter-racial ratio by both methods, namely, 1:1.414 and 1:1.49, respectively.

In *Anomalapteryx didiformis*, the diameters of the PB are 8.5, 7, 8 mm., the cube, 476 cmm.; the telencephalic cube is 29.500 cmm. The proportion of PB size to forebrain size, therefore, is 1:62 (1:67 in the ostrich endocast RCS, D 155). In *Dinornis maximus*, the figures are 12 x 12 x 14 mm. = 2016 cmm. and 68.880 cmm.: the proportion is 1:34. In relation to forebrain size, the pituitary body of *Dinornis* thus is found to have had almost twice the size of an *Anomalapteryx* PB. The ratio *Anomalapteryx*:*Dinornis* is: body height, 1:2.1; forebrain volume, 1:2.2; but PB volume, 1:4.2.

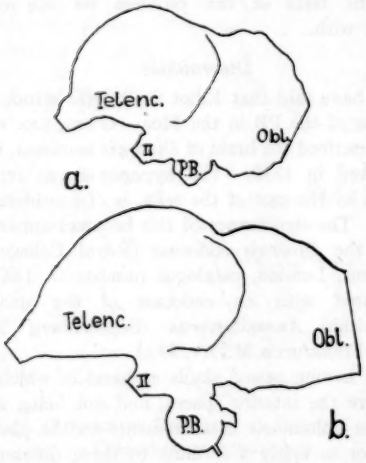


FIG. 2. OUTLINES OF ENDOCRANIAL CASTS OF (a) MULLERORNIS AGILIS (b) AEPYORNIS MAXIMUS

Left side views, two-thirds natural size. In (b) the cranio-pharyngeal canal is seen to open into the pituitary fossa from below, the carotid artery canal from behind.

Aepyornithids

It is true that we do not know the size of the individuals which furnished endocasts of brain cases either in the dinornithids or the aepyornithids. However, the author's investigation of 6 aepyornithid brains belonging to 4 species (Edinger '42) showed that two brains of one species are almost exactly alike, in spite of the size variability within aepyornithid species. Only one brain of each species was complete with PB.

Seen from above, these casts are rather similar to each other and to ostrich brains. The lower side reveals striking differences: the PB of the ancestral genus *Mullerornis* is the size of a blueberry (384 cmm.), that of the largest *Aepyornis* species, *A. maximus*, is the size of a cherry (3038 cmm.). The PB volume compares to the forebrain volume, with rising body size, as follows: *Mullerornis*, 1:102; *Aepyornis hildebrandti*, 1:82; *Aepyornis medius*, 1:36; *Aepyornis maximus*, 1:24!

When reading the table of interspecific ratios given in Table 1 (computed from numbers to be published in Edinger '42), the following points should be born in mind:

1. Below the stalk, which is not included in the measurements taken, the PB of *Aepyornis maximus* bulges out to form a globe, while those of *Mullerornis* and the smaller *Aepyornis* species are somewhat flattened antero-posteriorly; that is, the computation of the "cube" exaggerates the size of the PB more in the case of the smaller species than in the giant, the relative PB volume of which would therefore appear even larger had the actual volumes been measured.

TABLE 1

Interspecific ratios

	BODY-HEIGHT	FOREBRAIN-VOLUME	P.B.-VOLUME
Mull.:*Aep. hild.*	1:1.1	1:1.6	1:2.0
Mull.:*Aep. med.*	1:1.4	1:2.0	1:5.6
Mull.:*Aep. max.*	1:1.7	1:1.8	*1:8.0*
Aep. hild.:*med.*	1:1.3	1:1.2	1:2.8
Aep. hild.:*max.*	1:1.6	1:1.1	1:4.0
Aep. med.:*max.*	1:1.2	1:0.9	1:1.4

2. The body-heights are two-dimensional measurements and their comparison does not express the increase in body-volume in the evolution of the aepyornithids; this, naturally, was greater. However, height-comparison throws more light on the respective body-volume of these animals of identical build, with so small a trunk between such enormous legs and neck, than it would in almost any other animal. The numbers in the first column of the table rely on no more than the following mounted skeletons:

Mullerornis agilis: Tananarive (Madagascar), 148 cm.

Aepyornis hildebrandti: Tananarive, 165 cm.; London (England), 158 cm. = ~ 160 cm.

Aepyornis medius: no skeleton mounted; 211 cm. was computed from medium height of *Aep. max.* by the proportion of the medium tibiotarsus lengths of the two species.

Aepyornis maximus: Tananarive, 221 cm.; Paris (France), 300 cm. = ~ 260 cm.

These figures are so striking that we may draw the following conclusions although they are based on but one brain case of each species:

With increasing body-height in aepyornithid birds, the forebrain volume increases at a slightly higher rate than does body-length (but presumably at a lesser rate than does body-volume) only when the primitive genus is compared with the advanced genus. Within the genus which developed giantism, forebrain increase stays behind increase in body-height. Meantime *the PB increases at a much greater rate than does the body, manifesting almost 4½-fold the increase of forebrain volume in a comparison between the small genus and the largest giant species.*

Manifold though the activities of the PB are, the evolutionary trend in aepyornithids shows that this hyper-development of the PB was connected with their natural giantism. Even without the possibility of histological examination we are entitled to assume that the striking enlargement of these fossil pituitary fossae was due to an enlargement of the glandular lobe of the long-vanished PB.

Characters of subfossil ratites other than size likely to be due to hyper-activity of the PB

It has long been known that the volume of *eggs* of all *Aepyornis* species, above and below ostrich size, is much larger than that of ostrich eggs. The diameters of *Aepyornis* eggs are 280–340 and 213–245 mm., those of ostrich eggs 150–155 and 110–130 mm. This now proves to be a natural parallel, on a grand scale, to the effect on eggs of experimental hyperpituitarism: the eggs of pituitary-fed hens were over ⅓ heavier and ⅓ larger than the eggs of controls (Gutowska).

Together with their usually large size, there is one other characteristic distinguishing ratites from flying birds which is influenced by pituitary hormones—their *plumage.* Plumage development is controlled by the thyroid, the action of which, however, is regulated by the PB. Hypophysectomy in adult pigeons was followed by heavy moulting (Hill); the feathers of chickens hypophysectomized as embryos were shorter and less well developed, their sheaths were thicker and tougher and did not release the barbs as easily as in controls (Fugo). Implantation of anterior lobe stimulated feather regeneration (Voitkevic). Likewise, in human pathology, reduction of pituitary function causes loss of hair, while increase in hair-thickness and of the areas of hair-distribution (hypertrichosis) is observed in more than half the cases of giantism and acromegaly. Thus the fact that *Dinornis,* according to the numerous pits for feather insertion found in the metatarsal integument, must have been feathered down to the toes (Owen, 1883), and the peculiar "hair-likeness" and luxuriance of the plumage of the large ratites, now appear as a natural parallel to human hyperpituitary hypertrichosis. The looseness of the ratite feather barbs obviously is a natural counterpart to Fugo's experiment. The plumage of the aepyornithids is not known, but feathers of *Dinornis* have been found; they are soft, their barbs do not cling together to form a vane but are loose, filamentary: just the opposite to the feathers of Fugo's hypophysectomized chicken.

From the ecological viewpoint, this kind of feather is just one of the characteristics of birds unable to fly, and so is their size. How very far we are from being able to discriminate cause and effect, from knowing what is primary and what is secondary, is obvious from the existence of Lowe's doctrine according to which the ratite type is primitive, and branched off the main bird stem before flight was developed. If this were so, then, from the standpoint of the present investigation, we certainly could not consider the ratite feathers as signs of a kind of pituitary "disturbance" for they would be primitive, no "Zuruecksinken auf den Typus der Halbdune" (Stresemann). While agreeing with Romer's ecological interpretation of the origin of flightless birds, namely, that birds were liable to return to ground life in areas free from enemies (that is, areas in which extravagant hyperpituitarism and hypopituitarism (island dwarfs!) could also develop without immediately endangering the species), we note that no less an ornithologist than Stresemann forms just the reverse conception. In his opinion, the loss of the power of flight was the inevitable consequence of increase in body-size. From our point of view, this would mean nothing less than that the development of the ratite bird type was due to the activity of the pituitary gland!

Wiman (see Edinger and Wiman) has discovered a canal running from the nethermost pit of some *Aepyornis* (but no *Mullerornis*) pituitary fossae downwards and slightly backwards to the palate. The "venous foramen" on the lower side of the basisphenoid and the "mid-vertical canal" described and figured by Owen (1879, p. 263, 272, 280) in three *Dinornis* species show that such

persistence of the cranio-pharyngeal canal occurred in the other subfossil giant ratite family too. There is no record of this feature in other birds. Jaekel's search for the cranio-pharyngeal canal in present-day reptiles succeeded in discovering it only in three individuals; it may be significant that these were one alligator, one turtle of the large species *Chelone midas* whose shell reaches 130 cm. in length, and one lizard of the largest tejid species *Tupinambis teguixin* which is almost 1 m. long. We mentioned above that this embryonic character was retained in the largest-known, thus doubtless hyperpituitary, *Ichthyosaurus* (according to Fraas: *Gefässkanal*, p. 15), but also in "smaller" Ichthyosauri which, however, would have been considered giant reptiles had they lived to-day. It is certainly striking that the same is the case in Plesiosauria. The basisphenoid foramen described by White ('35) in the largest known plesiosaurian, the 372 cm.-skull of *Kronosaurus*, exactly corresponds to the pharyngeal opening of the canal descending from the ichthyosaurian fossa hypophyseos, and so does this foramen in the 68 cm.-long skull of *Macroplata* (White '40). As "extraordinary, . . . unique for *Trinacromerum* and *Polycotylus* among Plesiosaurs" this same foramen had been mentioned by Williston; it thus existed in a third plesiosaurian family, in animals of 3 m. body length. A median foramen in the palate of the type skull of the largest pterosaurian, *Pteranodon ingens*, is regarded as *Hypophysenloch* by Versluys (p. 758); in my opinion, however, the position of this vacuity (in front of the orbits in an animal whose brain lies behind the orbits) forbids this interpretation. On the other hand, a persistent cranio-pharyngeal canal is observed in all skulls of one giant dinosaur family, the Atlantosauridae.

It thus appears that persistence of the embryonic cranio-pharyngeal canal is much more common in giant birds and reptiles than in small ones. Should more material prove this to be true, the canal might be considered another sign of sauropsid hyperpituitarism.

There is also one record of the canal in an adult giant whale (*The Pituitary Gland*, Fig. 93a). On the other hand, it follows from Cave's statistics of the occurrence of the canal in higher primates that within a non-hyperpituitary group of mammals the frequency of persistence of the canal is by no means proportionate to body-size; the canal was present in 0.2 percent of the 5000 human skulls investigated by Cave, while the percentage in his ape material was: Orang, 14 percent; Gorilla, 35 percent; Chimpanzee, 64 percent.

IV. MAMMALS

The very name "sella turcica," derived from human osteology, indicates that the mammalian PB does not possess an actual bony capsule (and the term should not, in the writer's opinion, be applied to such fossae as are found, e.g., in birds). Not even the clinoid processes transversely bordering the laterally open "saddle" are present in every mammal. De Beer's description of the complete absence of a dorsum sellae in *Sorex* (1929: "the floor of the pituitary fossa—if it is permissible to speak of such a structure in *Sorex*—passes insensibly back into the basal plate") is rendered particularly instructive for the palaeo-endocrinologist by the addition of a list of mammalian genera exhibiting a similar state as well as a list of genera with a well-marked dorsum sellae. The former belong to the most primitive orders, Monotremata, Marsupialia and Insectivora, and to Sirenia and Edentata. The latter are Rodentia, Carnivora, Ungulata and Primates. But in the latter orders too, the palaeo-neurologist may find on the base of an endocranial cast only a low, ill-delimited protuberance representing the shallow depression in the sphenoid, upon which, rather than in which, the gland lay in the living animal. Furthermore, there are also mammals lacking any trace of a sella.

Thus, as far as Mammalia are concerned, the proposed investigation rests mainly with the neozoologist. Fortunately, some information on the PB of living mammals has already been published which yields results when viewed from our present standpoint. On the other hand, a great proportion of the existing endocasts of fossil mammals was described at the time when anatomists were mainly interested in forebrain convolutions, hence they published only top-view illustrations, and scarcely mentioned a single feature of the brain base.

This is, for instance, true of the description of the endocast of the Pleistocene marsupial *Thylacoleo* (of lion's size). The specimen in the endocast-collection of the Royal College of Surgeons of England shows, however, that this giant's PB must remain unknown—only the dorsum sellae has left a mark. The case of the cranial cavity of the living *Phascolomys* is entirely flat in the

pituitary region, while that of the giant kangaroo, *Macropus giganteus*, bears a well-delimited prominence.

From the endocast of *Tillotherium*, the Eocene insectivore of bear-size, nothing but an extremely ill-defined sella can be inferred. In accordance with Wislocki's finding of extremely shallow sellae in living sloths ('38), the pituitary area is flat in endocasts of fossil Edentata; yet the Gravigrada include such contrasts as the lightly built Miocene types and the stout Pleistocene *Megatherium* of 6 m. body-length.

Some Carnivora endocasts show no distinct pituitary protuberance (*Canis*, *Ursus*, *Meles*), some an ill-delimited one (*Lutra*, *Ailuropus*), and some obviously reproduce the distinct form of the PB: *Ailurus*, and most strikingly, *Felis tigris*. This tiger's PB was 13 mm. long and 10 mm. broad. The cat's PB measures 4 x 4 x 2–3 mm. (Trautmann) and thus is no smaller relatively than the tiger's. Similarly, Robb's comparison of the PB:body-weight ratio within one living rodent species demonstrated that the same decrease in relative PB-weight as takes place during growth in the small Polish rabbit and the giant Flemish rabbit is observed in the comparison of the adult forms; the relative PB-weight is even larger in the full-grown "dwarf" than in the "giant." If, however, comparison is made between the endocasts of various rodent genera, the pituitary region is seen to be flat but for one striking exception. This concerns the most bulky living rodent, *Hydrochoerus* (1 m. long, ½ m. high), which has, below a forebrain 65 mm. long, a pituitary protuberance 12 mm. in length.

The coin-shaped PB of the halicorid Sirenia makes hardly any impression in the flat sphenoid bone—but here too we encounter one significant exception. On endocasts of the giant seacow, the 7–10 m.-long subfossil *Rhytina*, there are slight hypophyseal elevations measuring no less than 21 x 33, 28 x 35 and 29 x 29 mm., while forebrain-lengths are 120–123 mm.

One of the few differences between the endocranial casts of the Eocene oldest sirenian and oldest proboscidean genera is that the latter has a prominent PB 14 x 9 x 4 mm. In the endocast of an *Elephas*, however, the pituitary region is indistinctly modelled. From a figure of an elephant brain (Smith '02), PB length and breadth have been measured at 40.3 and 24.5 mm. respectively. Likewise, Wislocki ('39) found the diameters of the PB of an adult Indian elephant 42 x 26 x 12, and he states that the proportion of its 7.53 g. weight to body-weight is no larger than in the hog (0.0002 percent = 1:50,000). But in the present context it appears significant that the neural lobe is very much smaller than the glandular lobe, their weight-ratio being 1:8.4. The only other record on the elephant PB is macroscopical only and refers to a 25-day-old calf (Dexler '07); the diameters are 24 x 16 x 6.

In a survey of the Roy. Coll. Surg. ungulate endocasts, the size of the pituitary protuberance in *Hippopotamus* at once strikes the eye. Its diameters are 27 x 25 x 17 mm. (forebrain-length 117 mm.), while the base of a *Sus scrofa* cast, with a forebrain of 86 mm. in length, is quite flat and unaffected by the gland, which measures in the pig 8–10 x 7–8 x 6–7 mm. (Trautmann). Most endocasts of artiodactyls bear some impression of a sella, but again that of a giant—the Pleistocene giant deer, *Megaceros*—is arresting for its distinctly modelled, large pituitary protuberance; this has a steep front of 13 mm. depth, a length of 28 mm., and a breadth of 22 mm., but it is, of course, not so well delimited laterally as in the other directions (forebrain-length 125 mm.).

The rhinocerid sella space is confluent with the chiasmatic groove; it thus cannot be measured on casts. In Milne-Edwards' sagittal sections of skulls of the Pleistocene *Rhinoceros tichorhinus* and a *R. unicornis*, the sella is deeper and longer (in relation to forebrain length: 161 and 131 mm., respectively) in the larger animal. Prof. W. K. Gregory of New York was so kind as to examine together with the present writer the base of the endocast of the largest known land-mammal, the Oligocene rhinocerid *Baluchitherium*. This giant had a forebrain only 125 mm. long in its 125 cm. skull. We found the PB ill-defined but apparently large. It seems to have extended over a space of approximately 45 mm. behind the optic foramen; the deepest point of the sella, 5 mm. below the brainbase, is 25 mm. behind the base of the optic foramen. This statement will, of course, become of value only when the PBs of the variously sized living rhinoceroses will have been investigated.

The sella of living horses is known to be extremely shallow; endocasts have no pituitary prominence. No endocast of the little ancestor *Eohippus* is known, and the descriptions of the *Mesohippus* brain neglect the base. When we

compare Trautmann's sagittal sections of the PB of ass and horse, we note a difference significant in the light of the present investigation. The diameters may be said to correspond to the different body-sizes: 17–19 x 16–18 x 4.5 in *Asinus*, and 17–24 x 20 x 6.5–8 in Trautmann's and 21 x 25 x 8.5 in Lothringer's *Equus*-specimens. But *the glandular proportion is much greater in the larger genus*; the pars nervosa is embedded in it like a stone in a fruit, whereas in the smaller genus it really is a posterior lobe, enveloped by the anterior lobe only at its rostral extremity. The same difference in composition is obvious from de Beer's sections of pig and ox PBs ('26); the pars glandularis is far larger in relation to the pars nervosa in the ox than in the pig. This phenomenon is most strikingly illustrated in the whales.

The order Cetacea contains, in the living whalebone-whales, the largest animals of all times. The reader who has followed our exposition so far will therefore learn without surprise that the cetacean PB is very markedly different from all other mammalian PBs in gross as well as microscopical anatomy. Rather will he be amazed at statements such as: "The underlying significance of the differences . . . remains obscure"; the suggestion that the pituitary modification meets needs of marine life; and the construction of a genetic linkage between those peculiarities of the PB in whales and the loss of their pelvic extremities —all published in the last decade.

The pituitary depression in the cetacean sphenoid is shallow in extant forms, and transverse processes are either hardly perceptible or else absent. Hence the pituitary region of endocasts of living whales is either smooth or shows a slight indistinct prominence. But on endocasts of the earliest whales one finds, apparently as one more trace of their carnivore parentage, an oval prominence at the site of the PB—in the Middle Eocene *Prozeuglodon* as well as in the Upper Eocene *Zeuglodon* (Dart; no measurements). In the Miocene *Prosqualodon*, the pituitary region of the brain case is flat.

The peculiarities of the cetacean PB are: the absence of a pars intermedia and of a residual lumen, and the *great size of the extremely vascular glandular lobe* which is completely separated by a dural fold from the small avascular neural lobe.

The total weight of the whale PB naturally is very small indeed if expressed in percentage of body-volume: 0.0027–0.0034 (man: ♂, 0.010; ♀, 0.014). But Valsö weighed anterior and posterior lobes of several *Balaenoptera sibbaldi* separately; maximum, minimum and medium numbers are 53.3–16.7–32.5 and 1.9–1.0–1.4 g., respectively. From these numbers the present writer has calculated the ratio of neural lobe to glandular lobe, as: maximum, 1:28; minimum, 1:16.7; medium *1:23*. The last-named (medium) proportion also results from Wislocki and Geiling's weights found in a *Physeter* of 45,000 kg. body-weight: pars posterior, 0.55; pars anterior, 12.7 g. (1:23), and likewise from their *Balaenoptera physalus* weights: 1.4 and 32.5 (1:23). Great though the variability in these weights is, *no such ratio is found in any other PB investigated*. From values compiled by Wislocki and Geiling, and van Dyke, the following ratios were calculated for comparison: man: ♂, 1:3.0–3.3, ♀, 1:4.5–4.8; cat: ♂, 1:2.2, ♀, 1:1.8; rabbit: ♂, 1:3.6, ♀, 1:5.1; rat: ♂, 1:4.5–7.5, ♀, 1:5.7–12.2.

If Geiling and Robbins' dorsal views of the intact PB of adult specimens of five cetacean genera (*The Pituitary Gland*) are viewed from our present standpoint, they at once show that the peak of size discrepancy between the two pituitary lobes is reached in the largest genera. Each figure shows the neural lobe lying on a glandular lobe of similar contours like a small object on a large cushion. But the transverse diameters of the neural and glandular lobes, as taken from the figures, are:

Denticeti:

Tursiops truncatus (maximum body-length: 4 m.): 6 and 10 mm. = 1:1.7

Delphinapteras leucas (6 m.): 11 and 23 mm. = 1:2.1

Physeter macrocephalus (23 m.): 3.5 and 21.5 mm. = 1:6.1

Mysticeti:

Balaenoptera physalus (24 m.): 7.5 and 24 mm. = 1:3.2.

Second specimen: 8.5 and 26 mm. = 1:3.1

Balaenoptera sibbaldi (31 m.): 7.5 and 35 mm. = 1:4.7.

These proportions of transverse diameters are not, of course, the proportions of lobe volumes, the discrepancy of which is far greater. In a side view of a *Physeter* PB, the neural lobe is seen as a thin tongue lying on the huge ball of the glandular lobe. But even the diameters show that the characteristic described as particularly *striking* and *obscure*, namely the relative size of the growth-promoting lobe, is the *more striking* within each suborder, the larger the body-size attained in the species, and

therefore *not obscure*. The phenomenon is, in the writer's opinion, fully explained by the fact that the order in which these peculiar PBs occur is the order in which the largest animals developed. Judging from the anatomy of the PB in the porpoise, it seems that a group which is prone to develop giant forms may be provided with a relatively large glandular lobe in its smaller representatives too.

The largest known primate was the Pleistocene *Megaladapis* whose skull was over 30 cm. in length—like *Aepyornis*, a native of Madagascar. Unfortunately, an endocast exists only of the upper part of the brain case. The endocranial casts of *Homo primigenius* likewise do not include the PB.

V. THE RELIABILITY OF THE PALAEO-ENDOCRINOLOGICAL CONCLUSIONS

Doubts have been expressed regarding the reliability of the palaeontologists' inference from the size of the pituitary fossae to their contents. They can now be considered resolved by the data given above, at least in so far as the size differences between the fossae of small ancestors and truly gigantic descendants are concerned. The increase in size, relative to brain size, of the latters' pituitary fossae cannot be due to anything but an enlargement of the growth-promoting glandular lobe of the PB.

Certainly the fossa contains, apart from the pars glandularis proper: meninges, vessels, sometimes cartilage, (in mammals) part of the tuber cinereum, sometimes part of the infundibulum which may contain a cavity, two further but smaller epithelial parts, viz., pars intermedia (absent, e.g., in birds and whales) and pars tuberalis (absent in certain lower vertebrates and in sloths), and, always, a pars neuralis. The latter has recently been found to be another gland of internal secretion (van Dyke, II, p. 291); its hormones, however, influence but the movements of the uterus, blood pressure, and diuresis—on experimental removal of the neurophysis alone, no visible function is suspended, and of course the body is not changed. The changes in body build consequent on radical hypophysectomy are, therefore, due to the loss of the pars glandularis.

Outstanding among these changes is the cessation of growth, although about 15 different hormones are ascribed to the gland. Outstanding among the differences between fossil vertebrates, in the phylogeny of which the increase in fossa hypophyseos volume far surpasses the increase in volume of the rest of the neurocranium, is the difference in body-size.

It is true that differences have been found between the PBs of small and large related living animals which evade palaeontological investigation, namely, different proportion of the lobes within the pituitary compound, and differences in the histological structure of the glandular lobe. No volumetric comparison of PB or fossa would reveal an increasing preponderance of the glandular, growth-promoting lobe such as is observed in a comparison of the PBs in the whales with increasing body-size. The same would, of course, apply to the two pigeon races of 28 and 55 cm. body-length, the PBs of which have been compared by Rost. He found a considerable amount of colloid-filled cysts in the PB of the smaller race which he regards as holding back in the gland hormones not needed in the formation of the smaller body. Rost's following statement recalls our comparative observations on whales:

> "Der Vergleich des glandulären Anteils der Hypophyse lässt zunächst einen wesentlichen Unterschied im Hinblick auf ihre Volumina erkennen, welche in einem Verhältnis von etwa Rö:Mö [larger to smaller race] = 3:2 stehen. Dieses Verhältnis ist in Übereinstimmung zu bringen mit dem Unterschiede der Körperdimensionen" (p. 263).

Unfortunately, neither in rabbits, whales, nor pigeons (apparently the only living animals in which so far PBs of small and large representatives have been compared) has the size ratio between PB and brain been investigated. While these comparisons furnish no direct parallels to our results of endocranial cast measurements, the finding of extraordinarily large glandular lobes in the giant whales and pigeons indirectly stresses our assumption that a larger pituitary fossa of a larger animal signifies an enlargement of no other part of the PB than the glandular lobe.

It follows from the various evidences now at hand that Nopcsa was perfectly right when correlating dinosaurs' giantism with their hypertrophic PB. Yet only recently an objection to Nopcsa's theory has been voiced which must be discussed since it comes from the discoverer of the largest reptilian PBs, Janensch. "Die bekannte Hypothese, die die Riesengrösse der Sauropoden mit einer angenommenen Hypertrophie der Hy-

pophyse in Zusammenhang bringt, scheint mir bei zahlenmässiger Prüfung an Wahrscheinlichkeit einzubüssen."

It is true that the biggest of the three contemporaneous sauropods investigated by Janensch did not have the largest fossa, neither absolutely nor in relation to brain-size. But not even Nopcsa would have expected this; even when referring to established ancestry, he qualified his statement of increase in PB volume to "on the whole".

Apart from his specific discovery that the PB of the largest sauropod individual was not the largest in the suborder, Janensch's general reason for doubting Nopcsa is his objection to comparisons of brain volume and PB volume. This he thinks misleading because the brain of the giant sauropods "naturgemäss relativ klein war"—as, let us add, was any part of their relatively tiny head. While we regard it as fortunate to find the growth-promoting organ so near to the brain, the prototypal organ which is least involved in body enlargement, Janensch stresses the importance of comparing PB-volume with body-volume. His above-quoted conclusion rests on the fact that the PB compares to the body: in pigeons, in the proportion of 1:23,000; domestic fowl, 1:110,000; ducks, 1:200,-000; but 1:800,000 in *Barosaurus* and 1:1.800,-000 in *Brachiosaurus* whose PB thus appears to be small.

To relegate these figures to their right place in our argument, it is hardly necessary to point to the mechanical impossibility of finding room, in the miniature head of a bulky sauropod, for a PB as large in relation to body-size as is provided for in the big skull of a slender bird. It is sufficient to stress the ordinary variability of the volume of the PB, the relations of which are far from being restricted to growth alone. For instance, the ♂/♀ difference in children from birth to five years of age is no less than a PB-weight:body-weight ratio of ♂♂ 1:44994/♀♀ 1:3252 (Lucien). The average weight of the PB in a nulliparous woman is 61.8 centigrams, in primiparae it is 84.7 cg., in multiparae, 106 cg.; the enlargement takes place in the anterior lobe only, does not affect the length of the PB (hemmed in by the sella), but increases the breadth from 14.4 to 17.5 and the height from 5.9 to 8.0 mm. (Erdheim and Stumm, quoted from Wittek). Wittek's examination of 734 cattle showed that while there is a steady increase of pituitary weight with increase of body-weight in both sexes, two 3-year-old bulls of the same body-weight had PBs of 1.90 and 3.02 g., respectively; two such cows, even 2.6 and 6.2 g., respectively.

It follows that comparison of conditions in related, contemporaneous, single individuals cannot impair a statement which applies to extensive phylogenetic development: namely, that small dinosaurs had relatively small PBs while PB-volume increased, on the whole, in direct proportion to the development of their giantism.

Consequently, it may well be that when the suggestions made in this paper are carried out by neozoologists, the differences in structure and in size relative to the brain between the PBs of small and gigantic genera expected by the palaeozoologist will fail to be found. Such cases are already established; but they only recall the palaeo- and neo-zoologists' different views of the inheritance of "acquired characters": the palaeozoologist firmly believes that he can follow this phenomenon *throughout the ages*, to which the neo-zoologist retorts that it cannot be demonstrated *in our lifetime*.

The difference between the PB of a small ancestral genus and that of its gigantic descendant does indeed not seem to be paralleled in the volume of the PB of *Felis domestica* and *Felis tigris*, our contemporaneous species of one genus on the same evolutionary level. Robb has already denied any difference between the relationship of PB-weight and that of eyeballs, etc., to body-weight, on the ground that there is no difference in the mass of the PB that can be correlated to the size differences attained in two breeds of one and the same living species, the domestic rabbit. In both these cases, the composition of the PB is not known; furthermore, the animals compared differ exclusively by their size. It is, however, not only size by which *Aepyornis* is distinguished from *Mullerornis*, but there is also a progressive increase of, for instance, bone density in the family. Not only because of their size are the sauropods called "dragons". A long evolution led them away from the unspecializied reptilian type and size of their ancestors. The hippopotamus is not just an enlarged pig as the tiger is an enlarged cat; the sperm whale is not an enlarged porpoise but a porpoise further developed in many ways. It remains to be investigated which kind of size differences are always paralleled by definite size differences of the PB.

No external cause can be made responsible for the development of either individual or phylo-

genetic hyperpituitary giantism. Bailiff's experiments have shown that the PB actually is influenced by external agents: microscopic changes and hypersecretion were produced in the glandular but not in the neural lobe by exposure of rats to cold for 9–56 hours. But human as well as animal giants with extraordinarily active PBs have been observed to develop in their normal surroundings. The sudden manifestation of human hyperpituitarism is a pathological phenomenon to the medical profession whose object is present-day man; yet the palaeontologist notes that it is apt to become a hereditary disposition. The occasional occurrence of chickens with ostrich-like feather pecularities, however, is a mutation for the zoologist (Murphy); PB and thyroid may be supposed to be the primarily affected organs. Likewise, one tadpole of one frog family in Hahn's aquarium grew to double, and three tadpoles grew to 3½ times the size of the others, and they exhibited very marked anterior lobe hyperplasia.

Phylogenetic trend towards giantism also developed in every kind of environment, through such still unexplained changes in the germ plasm. Its occurrence can all the less be intrepreted in terms of Lamarckism since the accompanying bone changes vary from retardation of epiphysis ossification with increased massiveness of the long bones (sauropod dinosaurs) to an abundance of bony outgrowths of the skull (ceratopsid dinosaurs, giant titanotheres, and rhinoceroses) and osteosclerosis (whales). This recalls the different response of different animals to experimental hyperpituitarism.

Whichever conditions may one day be found to start and pave the way for the formation of giant animals, the fact can to-day be considered established, by the palaeontological evidence described above, that phylogenetic evolution of definitely gigantic types is accompanied by a conspicuous enlargement of the anterior pituitary lobe.

VI. SUMMARY

Clinical experience shows that in human giants the glandular lobe of the pituitary body is abnormally enlarged. Experimental administration of glandular lobe extracts stimulates body-growth to such an extent that the animals may grow beyond the maximum normal size of their species. The present investigation furnishes some parallels in natural evolution: phylogenetic development of giantism in reptiles, birds, and mammals was found to be accompanied by a striking enlargement of the pituitary fossa which can only be due to an enlargement of the glandular lobe which secreted the growth hormone.

In giant Jurassic dinosaurs, the volume of the fossa hypophyseos may amount to 10 per cent of the brain-case volume.

Among the subfossil aepyornithids, pituitary volume compares to forebrain volume as 1:102 in the ancestral genus *Mullerornis* (body-height:148 cm.); within the genus *Aepyornis*, the ratio rises from 1:82 in *A. hildebrandti* (160 cm.) to 1:36 in *A. medius* (211 cm.), and to 1:24 in *A. maximus* (221–300 cm.). While body-height was about doubled, the volume of the forebrain increased by four fifths, but PB- volume became eightfold. The extraordinary size of the aepyornithid eggs and the loose luxuriant plumage of the large ratites now appear as signs of hyperpituitarism.

Similar hypophyseal development as in the aepyornithids is observed in the dinornithids. The small dinornithid *Anomalapteryx* had a relatively larger PB than the larger ostrich; the same was the case in the aepyornithid of ostrich size, and the composition of the porpoise PB points in the same direction: phyla apt to develop giant forms may be provided with a proportionately large glandular lobe also in the smaller representatives. The extraordinary size of the cetacean, particularly of the giant whales' anterior lobe is unparalleled.

Although the sirenian skull usually possesses no pituitary groove, the PB of the 10 m.-long subfossil *Rhytina* left an extensive impression in the sphenoid bone. A comparison of a large series of mammalian endocasts has shown that the PB of giant forms may model the skull base in orders which possess no sella.

The present report is mainly based on endocranial casts, mostly of single representatives of the species. Its significance remains to be tested, as far as this is possible within the extant animal world, by comparative investigation of pituitary glands.

The author is deeply indebted, for the hospitality shown to her in London, during the studies undertaken for this paper, to Dr. C. Forster-Cooper, F.R.S., Director of the British Museum (Nat. Hist.), and to Mr. W. N. Edwards, Keeper of the Department of Geology, for permission to work in the Department, as well as to Dr. A. T. Hopwood for his help with a

preliminary manuscript; also to Dr. A. J. E. Cave, Assistant Conservator of the Museum of the Royal College of Surgeons, for permission to study this museum's collection of endocranial casts (the brain collection was stored in a bomb proof cellar). Prof. C. Lamberton, of the Académie Malgache, and Prof. C. Wiman, Upsala, my collaborator on the Académie's aepyornithid specimens, were so generous as to allow me to mention data not yet published in the Académie's Memoirs.

LIST OF LITERATURE

BAILLIF, R. N. Microscopic changes in the hypophysis of the albino rat following exposure to cold and their relationship to the physiology of secretion. *Amer. Jour. Anat.*, 62, 475–495, 1938.

BAUER, J. Hypophyse und Wachstum. *Klin. Wnschr.*, 9, 625–628, 1930.

DE BEER, G. R. The comparative anatomy, histology and development of the pituitary body. *Biol. Monogr.*, 6, I–XIX, 1–108, 1926.

——. The development of the skull of the shrew. *Phil. Trans. Roy. Soc. London (B), 217*, 411–480, 1929.

BENEDICT, E. B., T. J. PUTNAM, and H. M. TEEL. Early changes produced in dogs by the injections of a sterile active extract from the anterior lobe of the hypophysis. *Amer. Jour. Medic. Sci.*, 179, 489–497, 1930.

BROWN, B., and E. M. SCHLAIKJER. The structure and relationships of *Protoceratops*. *Ann. New York Acad. Sci.*, 40, 133–266, 1940.

CAVE, A. J. E. The craniopharyngeal canal in man and anthropoids. *Jour. Anat.*, 65, 363–367, 1931.

DEXLER, H. Zur Anatomie des Zentralnervensystems von *Elephas indicus*. Arb. neurol. Inst. Wiener Univ., Festschrift Obersteiner, 1907. (Quoted from notes.)

VAN DYKE, H. B. The Physiology and Pharmacology of the Pituitary Body. *Chicago*. I: 1936. II: 1939.

EDINGER, T. Die fossilen Gehirne. *Berlin*, 1929, and: *Erg. Anat.*, 28, 1–249, 1929. (Cf. Bibliography.)

——. Palaeoneurologie. *Fortschr. Palaeont.*, 1, 235–251, 1937. (Cf. Bibliography.)

——, and C. WIMAN. Le crâne et l'encéphale des Aepyornithes. *Mém. acad. malgache* (Not yet printed).

EVANS, H. M. *et al.* The growth- and gonad-stimulating hormones of the anterior hypophysis. *Mem. Univ. Calif.*, 11, 1–446, 1933.

FRAAS, E. Die Ichthyosaurier der süddeutschen Trias- und Jura-Ablagerungen. *Tübingen*, 1891.

FUGO, N. W. Effects of hypophysectomy in the chick embryo. *Jour. Exper. Zool.*, 85, 271–297, 1940.

GUTOWSKA, M. S. Effects of prolonged oral administration of large doses of pituitary anterior lobe to laying hens. *Quart. Jour. Exp. Physiol.*, 21, 197–216, 1932.

HAHN, A. Einige Beobachtungen an Riesenlarven von *Rana esculenta*. *Arch. mikr. Anat.*, 80, 1–38, 1912.

HANDELSMAN, M. B., and E. F. GORDON. Growth and bone changes in rats injected with anterior pituitary extract. *Jour. Pharmac. Exp. Therap.*, 38, 349–362, 1930.

HENDERSON, W. R. Sexual dysfunction in adenomas of the pituitary body. *Endocrinology*, 15, 111–127, 1931.

HERRICK, C. J. The amphibian forebrain. I. *Jour. Compar. Neurol.*, 37, 361–371, 1924.

HILL, R. T. *et al.* Hypophysectomy of birds. *Proc. Roy. Soc. London (B)*, 115, 402–409, 116, 208–236, 1934.

JAEKEL, O. Epiphyse und Hypophyse. *Sitz. ber. Ges. naturf. Freunde Berlin*, 1903, 27–58.

JANENSCH, W. Die Schädel der Sauropoden *Brachiosaurus*, *Barosaurus* und *Dicraeosaurus* aus den Tendaguruschichten Deutsch-Ostafrikas. *Palaeontographica, Suppl.* 7, 1.Reihe, Teil 2, 247–297, 1935.

KADANOFF, D. Über die Beziehung zwischen der Grösse der Sella turcica und der Schädelgrösse. *Anat. Anz.*, 87, 321–333, 1938–39.

KEITH, A. An inquiry into the nature of the skeletal changes in acromegaly. *Trans. London Med. Soc.*, 34, 90–119, 1911.

——. The evolution of human races in the light of the hormone theory. *Bull. John Hopkins Hosp. Baltimore*, 33, 155–159, 1911.

KÜENZI, W. Versuch einer systematischen Morphologie des Gehirns der Vögel. *Rev. Suisse Zool.*, 26, 17–111, 1918.

LAMBRECHT, K. Handbuch der Palaeornithologie. *Berlin*, 1933. (Cf. Bibliography.)

LARGER, R. Théorie de la contre-évolution ou dégénérescence par l'hérédité pathologique. *Paris*, 1917.

LOTHRINGER, S. Untersuchungen an der Hypophyse einiger Säugetiere und des Menschen. *Arch. mikr. Anat.*, 28, 257–292, 1886.

LUCIEN, M. Les poids, les dimensions et la forme générale de l'hypophyse humaine aux différents âges de la vie. *C.r. Assoc. anat.*, 13, 147–158, 1911 (Quoted from COVELL, *Amer. Jour. Anat.*, 38, 1927.)

MORTIMER, H. Pituitary and associated hormone factors in cranial growth and differentiation in the white rat: a roentgenological study. *Radiology*, 28, 5–39, 1937.

MURPHY, R. C. Discussion (of: W. K. Gregory: Origin of ratites and penguins). *Proc. Linn. Soc., New York*, 45–46, 11–17, 1935.

NOPSCA, F.v. Die Riesenformen unter den Dinosauriern. *Cbl. Min. Geol. Palaeont.*, 332–351, 1917.

OWEN, R. On Dinornis, Pt. 16. *Trans. Zool. Soc. London*, 7, 381–396, 1872.

——. Memoirs on the extinct wingless birds of New Zealand. *London*, 1879.

——. On Dinornis, Pt. 24. *Trans. Zool. Soc. London*, 11, 257–261, 1883.

PETERSILIE, Dissertation Jena 1920. (Quoted from DUERST, Grundl. d. Rinderzucht, *Berlin*, 1930.)

Pituitary Gland, The. An investigation of most recent advances. *Res. Publ. Assoc. Res. in Nerv. and Mental Diseases*, 17, I–XXIV, 1–764, 1938.

PUTNAM, T. J., E. B. BENEDICT, and H. M. TEEL. Studies in acromegaly. VIII. Experimental canine acromegaly produced by injection of anterior lobe pituitary extract. *Arch. Surgery*, 18, 1708–1736, 1929.

ROBB, R. C. Is pituitary secretion concerned in the inheritance of body-size? *Proc. Nat. Acad. Sci. Washington*, 14, 394–399, 1928.

ROMER, A. S. Vertebrate Palaeontology. *Chicago*, 1933.

ROST, H. Die Entwicklung der Hypophyse der Haustauben und ihre rassetypische Ausbildung bei der Römertaube und der Mövchentaube. *Zeitschr. wiss. Zool.*, 152, 221–276, 1939.

SMITH, G. E. Catalogue Physiol. Ser. Mus. Roy. Coll. Surgeons, England, 2, Second edition, *London*, 1902.

STERNBERG, C. M. A new species of horned dinosaur from the Upper Cretaceous of Alberta. *Canada Dept. of Mines, Bull.* 54 (*Geol. Ser.* 49), 34–37, 1929.

STRESEMANN, E. Aves. *Handb. Zool.*, 7, II, 1927–1934.

TRAUTMANN, A. Die makroskopischen Verhältnisse der Hypophyse einiger Säuger. *Arch. wissensch. prakt. Thierheilk.*, 35, 416–437, 1909.

UHLENHUTH, E. Experimental production of gigantism by feeding the anterior lobe of the hypophysis. *Jour. General Physiol.*, 3, 347–365, 1921.

VALSÖ, J. Der Hormongehalt der Hypophyse des Blauwals (*Balaenoptera sibbaldi*). *Klin. Wnschr.*, 13, 1819–1820, 1934.

VERSLUYS, J. Kranium und Visceralskelett der Reptilien. *Handb. vergl. Anat. Wirbelt.*, 4, 699–808, 1936.

VOITKEVIC, A. A. Die morphogenetische Aktivität der verschiedenen Teile der Hypophyse. VIII. Der Einfluss des Hypophysenvorderlappens auf die Schilddrüse und Federbildung bei Tauben. *C. R. acad. sci. URSS*, 17, 157–160, 443–444, 1937.

WHITE, T. E. On the skull of *Kronosaurus queenslandicus* Longman. *Boston Soc. Nat. Hist., Occ. Papers*, 8, 219–228, 1935.

——. Holotype of *Plesiosaurus longirostris* Blake and the classification of the plesiosaurs. *Jour. Paleont.*, 14, 451–467, 1940.

WILLISTON, S. W. North American plesiosaurs. *Trinacromerum*. *Jour. Geol.* 16, 715–736, 1908.

WISLOCKI, G. B. The hypophysis of the porpoise (*Tursiops truncatus*). *Arch. Surgery*, 18, 1402–1412, 1929.

——. The topography of the hypophysis in the Xenarthra. *Anat. Rec.*, 70, 451–471, 1937–1938.

——. Note on the hypophysis of an adult Indian elephant. *Anat. Rec.*, 74, 321–328, 1939.

——, and E. M. K. GEILING. The anatomy of the hypophysis in whales. *Anat. Rec.*, 66, 17–36, 1936.

WITTEK, J. Über das Verhalten der Rinderhypophyse bei den verschiedenen Geschlechtern, in der Gravidität und nach der Kastration. *Arch. Anat. Physiol., Anat. Abt., Suppl.* 1913, 127–152.

STRUCTURAL RELATIONS IN CELL RESPIRATION

By BARRY COMMONER

Department of Biology, Queens College, Flushing, New York

INTRODUCTION

THE living cell exhibits two striking and apparently contradictory properties. In the first place, the substances that make up living protoplasm endow it with a certain morphological stability, which expresses itself grossly in the well-known intracellular structures such as the nucleus, chondriosomes, plastids and so on, and more finely in the persistence of the physical and chemical properties of protoplasm through the environmental, developmental, and evolutionary changes to which it is subject. This stability of living organisms, and the relative independence of the cell from alterations in its environmental conditions (within certain limits), was one of the first of its properties to be recognized by biologists and led many to suppose that such effects could only be accounted for by a supernatural and directive "vital force." On the other hand, it was soon made abundantly clear that the apparent stability of the cell and of the whole organism is contingent upon a continuous interchange of matter between the cell and its environment—that life is characterized by the assimilation of substances from the outside world and the concommitant destruction and excretion of intracellular material and of protoplasm itself.

Thus, morphological stability and metabolic activity, while apparently antagonistic, are together the essential properties of all living things. To date it has been impossible to separate these characteristics, and the smallest independent unit of structure, the cell, is also the smallest unit which is capable of maintaining complete metabolic activity. However, in recent years with the development of analytical biochemistry, it has been possible to break down the cell, extract certain of its components, and reproduce *in-vitro* various fragments of the metabolic process. This type of work has accumulated a large body of data which are in the main limited to the destructive processes alone. Perhaps the best known and most important of these catabolic processes are those involving the oxidative degradation of organic metabolites, which in series make up "cellular respiration."

The very accumulation of these data has, in the last few years, forced upon research workers the problem of integrating this information and relating the separate reactions to the entire respiratory process in the intact cell. It has become generally recognized that the separate *in-vitro* data on the various extracted parts of the respiratory system do not in themselves provide an adequate picture of the behavior of this system in the cell itself. But there is a good deal of disagreement as to the manner in which these analytical data are to be related to the properties of the entire cell.

It has frequently been suggested, for example, that the total living system can be "reconstructed" by fitting together the various reactions which have been studied in extracts, as one would a jig-saw puzzle. Thus, according to D. E. Green (1) the biochemist must "resort to the disorganization of the cell in order to puzzle out the mechanisms of reaction."

The validity of this "reconstruction" method has been severely taxed by the evidence obtained from the extracts themselves. As will be shown below, these *in-vitro* data themselves necessitate the conclusion that the protoplasmic *structure* (which is destroyed in obtaining such data) plays the major rôle in orienting the metabolic reactions within the cell. Further, it will be seen that data obtained from intact cells often disagree with the behavior of reconstituted enzyme systems *in-vitro*.

On the other hand, a number of workers have suggested, on the basis of specific evidence, that the properties of cellular metabolic systems must

be strongly conditioned by the intracellular structure. Thus Warburg's earliest work on cell respiration was accompanied by a strong emphasis of the rôle played by the structural arrangements of the cell constituents (2). Batelli and Stern (3) spoke of two types of cell respiration, one related to the cell structure and the other to the "fluid" constituents. More recently, Korr (4) finds that "bioluminescence, like many other bacterial oxidative phenomena, is closely associated with cellular structure." Similarly, Stier and Newton (5) conclude that changes in the endoggenous metabolism of yeast are related to reorganization of the intracellular structure. Much of this type of implicit evidence has been discussed by Korr (6).

It is becoming increasingly clear that cell structure plays a major rôle in the orientation of cellular metabolic systems, particularly those concerned with oxidations. The literature contains much evidence obtained from intact cells that points to this conclusion. In addition there is a store of information concerning the properties of respiratory enzyme systems which have been extracted from the cell, and so freed from some of its structural limitations. It is our aim to correlate these two types of data with the purpose of describing what may be called the history or development of the structural properties of respiratory enzymes as they pass from the more "chemical" state of the *in-vitro* extract to their biological position in the intact living cell. It is hoped that such a discussion will provide at least a tentative indication of the structural orientations which appear to regulate the activity of cellular enzyme systems.

It is our purpose here to review certain of the data concerning the respiratory properties of both reconstructed systems and intact cells, with the view of demonstrating the relationship between these properties and the internal structure of the cell.

THE SEQUENTIAL NATURE OF THE RESPIRATORY PROCESSES

The net result of aerobic respiration in the cell is the combustion of an organic metabolite, the production of carbon-dioxide and water, and the consumption of oxygen. This process involves a series of oxido-reductions which can be very generally represented thus:

$$D\text{-}H_2 + C \rightarrow D + C\text{-}H_2, \quad C\text{-}H_2 + \tfrac{1}{2}O_2 \rightarrow H_2O + C$$

where $D\text{-}H_2$ represents the metabolite, D the oxidation products of the metabolite (eg. CO_2), C a reversibly oxidizable carrier in its oxidized state, and $C\text{-}H_2$ the carrier in its reduced state. Actually, the "carrier" (C) may be a long series of reversible oxido-reduction reactions. The result of this series of reactions is the transference of electrons, but as can be seen above, it is convenient to picture the process in terms of hydrogen transfer.

According to the "reconstruction" technique it is customary to interpret such a serial process in terms of the oxidation-reduction potentials of the individual reactions which constitute the chain. Thus, the generalized system above would be written:

$$1)\ D\text{-}H_2 \leftrightarrows D + 2H + 2\epsilon$$
$$2)\ C\text{-}H_2 \leftrightarrows C + 2H + 2\epsilon$$
$$3)\ H_2O \leftrightarrows \tfrac{1}{2}O_2 + 2H + 2\epsilon$$

The tendency of each of these reversible reactions to proceed in one direction or the other is expressed by the electron pressure which they produce or absorb, that is, by the oxidation-reduction potential (E_0). It is then postulated that the ordering of the entire sequence is due to the quantitative relations of the various reaction potentials involved. Thus in the case above, $E_0(3) > E_0(2) > E_0(1)$, and the sequence is thereby determined. It would follow from such an interpretation that the configuration of a chain of respiratory reactions depends on the relations of the E_0's of the various reversible oxido-reduction systems present in the cell.

The last conclusion is often put forward by adherents of the reconstruction school, although its limitations when applied to *cellular* conditions are also pointed out. However, a further examination of the data reveals that such reconstructed systems are more than merely limited in their application to the living cell. The *in-vitro* data themselves show that the most important factor controlling the ordering of the respiratory systems is the protoplasmic structure which is always destroyed in the course of such experiments.

It is clear that the oxidation-reduction potential indicates merely a *tendency* to react in a particular way. But actual reaction between processes (1) and (2), for example, does not follow from a relation of *tendencies*. In order that the electron transfer really occur, it is necessary that a molecule of $D\text{-}H_2$ collide with a molecule of C. That is, the ordering of the series $1 \rightarrow 2 \rightarrow 3$, depends on actual material contact between the reacting substances. The E_0 value of each oxidation-re-

duction equilibrium indicates which reactions are thermodynamically *possible*, but only those *will* occur which are also made possible by molecular collisions.

This requirement at once introduces, in a sense, the importance of structural relations. Even in a homogeneous system, say where substances A and B are dissolved in an inert solvent and $A+B \rightarrow C$, there is an element of "structure". This system is homogeneous if molecules of A and B are free to move about the medium in all directions. However, the occurrence of the chemical change ($\rightarrow C$) depends on the momentary loss of this directional freedom by a molecule of A and of B, that is, the reaction occurs only on *collision*. At the instant of collision, molecules A and B have a fixed spatial relation relative to each other and this relation results in the change to C or in their separation. The homogeneity of this system resides in the fact that the reacting molecules have three degrees of translational freedom, and that their rate of collision is therefore determined by a probability function which is directly proportional to the product of their concentrations. Yet the chemical process itself depends on a spatial or "structural" orientation of A and B, however transitory this moment of collision may be.

THE STRUCTURAL IMPLICATIONS OF HETEROGENEITY

In the case of reactions which occur in heterogeneous systems, such as obtain in the living cell (or in fact in cell extracts as well), the structural orientation, which in the homogeneous system is so transitory, becomes of the first importance.

To return to the generalized diagram of the respiratory process, it must now be pointed out that each step is mediated by a protein enzyme or by a carrier which is linked to a protein. Thus the process: $D\text{-}H_2+C \rightarrow D+C\text{-}H_2$ depends on the activation of the H atoms of the metabolite ($D\text{-}H_2$) by a *dehydrogenase* enzyme. Similarly the reaction $C\text{-}H_2+\frac{1}{2}O_2 \rightarrow C+H_2O$ depends on the activation of the molecular oxygen by the *oxidase* enzyme.

In fact every reaction that makes up the chain of respiratory processes involves one or more enzymes, and these reactions cannot proceed at any appreciable rate *in-vitro* in the absence of the enzymes. It is hardly necessary to point out how important this enzyme mediation is, except to recall that by this means are produced rapid chemical changes which would otherwise require extremely drastic conditions of temperature, pressure, and pH.

Every known respiratory enzyme (and every other enzyme) including those which have been successfully extracted and purified is at least in part protein. Usually there is associated with the protein a so-called prosthetic group which may be an organic compound containing a heavy metal (usually Fe or Cu) or a reversibly oxidizable dye. Many of the prosthetic groups and certain of the protein bases have been isolated and crystallized. Some of the prosthetic-group-protein compounds appear to be rather loosely bound, but in every case a specific protein is essential to the enzyme activity.

Solutions of such proteins have often been termed "micro-heterogeneous systems". This description is quite apt, in that the protein molecules while dispersed in the solution are so large, as compared to the substrate molecules, that they behave as though in a solid state. Here the spatial relations of the enzyme and substrate become of prime importance.

It is generally accepted that enzyme catalysis involves the formation of a substrate-enzyme complex. Since the enzyme particle is much larger than the substrate molecule (except in the case of extracellular proteolytic enzymes which act on entire protein molecules), this union occurs as a binding of the substrate molecules on the surface of the enzyme. Haldane (7) has calculated that an enzyme of molecular weight 60,000 and density 1.1 would have a surface of 9856 square Ångstroms and could probably hold about 150 hexose molecules. In order to undergo chemical change the substrate must be bound on the enzyme surface, but not all of the surface is catalytically active. Rather, in many cases, it has been found that the activity is restricted to a limited number of surface points. Thus, if saccharase or lipase is adsorbed on an inert substance such as alumina, the enzymatic activity is retained. On the other hand, if lipase is adsorbed on a fat, it loses its enzymatic activity. Thus, it appears that the active centers of the enzyme take part in the binding of its specific substrate.

Similarly, Quastel (8) has shown that the various metabolites which can be oxidized by bacteria are activated by specific dehydrogenases which are characterized by specific "active spots". In general it has been found that dehydrogenases exhibit a high degree of substrate specificity which appears to be dependent upon the presence of specific side-chains on the substrate molecule. In some

cases, enzymes exhibit a stereochemical specificity, as for example the d- and l-deaminases (Krebs (9)).

It becomes clear, therefore, that enzyme catalysis, even *in vitro*, depends on the spatial orientation of the enzyme and its substrate. Not only is it required that the substrate be bound at a specific spot on the enzyme surface, but its link to the enzyme also depends on the presence (on the substrate molecule) of a particular side-chain.

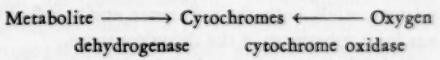
Here, then, the structural factor becomes strongly emphasized. In a homogeneous system the reacting particles have complete freedom of motion, except at the instant of collision. In a micro-heterogeneous enzyme system, the substrate molecules are still free to move about in solution. However, the enzyme is now in effect a two dimensional surface upon which the substrate molecules must become structurally oriented before undergoing any change. In such a system the substrate constitutes one reactant, and the *active-spots* of the enzyme the other reactant. Since the latter are *fixed* points on the surface of the enzyme particle, they cannot exhibit the statistical kinetic behavior characteristic of the free reactants in a homogeneous system.

This increase in structural rigidity is reflected in the kinetic properties of heterogeneous enzyme systems. In homogeneous systems the rate of reaction is proportional to the frequency of effective collision and is therefore proportional to the product of the concentrations of the reactants. However, in enzyme systems, while the rate of reaction is still proportional to the number of collisions, that is, to the number of substrate molecules combined with the active spots of the enzyme, the latter value is not always dependent upon the concentration of substrate in the medium. As the substrate concentration is increased from zero, the number of active spots combined with substrate will increase, but this will become limited by the rate of release of substrate molecules in the activated state. Finally, as the rate of collision of active spots with unactivated substrate molecules increases with the substrate concentration, a point will be reached where this rate is equal to the speed of release of the active spots. The rate of substrate activation is now at a maximum, and any further increase in substrate concentration will have no effect on the rate of activation. In this way, the rate of enzyme activity may become independent of the concentration of one of the reactants involved. The structural properties of the enzyme thus result in the characteristic relative independence of cellular activity from the outside environment. This phenomenon is characteristic of all enzyme processes, and led Michealis and Menten to the development of the theory of the enzyme-substrate complex.

The intrinsic properties of substances that participate in heterogeneous reactions are also influenced by the structural orientations to which they are subject. Thus, Kuhn and Boulanger (6) find that the E_0 of riboflavin phosphate (the prosthetic group of the yellow respiratory enzyme) is considerably more negative in value than the E_0 of the riboflavin-protein complex. Similarly Korr (11) has demonstrated the shift in E_0 value which occurs when various oxidation reduction systems are bound on surfaces. It must certainly be concluded that the thermodynamic properties of oxidation-reduction reactions become considerably altered when they function within the cell. This places a further limitation on the validity of sequential respiratory systems which are reconstructed from E_0 data obtained from various protein-free oxido-reduction reactions.

On the other hand, if we recognize the significance of the structural properties of the respiratory enzymes, it is possible to find a much stronger basis for the serial ordering of oxido-reductions in the living cell.

Thus far we have been considering only the relation between an enzyme and a single *substrate*. However, the sequential nature of respiratory enzyme systems makes it necessary for the constituent enzymes really to mediate *two* substrates. This is clearly illustrated in the case of the Warburg-Keilin respiratory system which is responsible for most of the oxidative activity of aerobic cells (for the sake of simplicity various intermediate carriers are omitted):



The metabolite is activated by its specific dehydrogenase and is oxidized by reducing the cytochrome (usually by way of the intermediate H transfer via a coenzyme). The reduced cytochrome is reoxidized by molecular oxygen through the mediation of the cytochrome oxidase. The oxygen molecules are bound by the oxidase but at the same time, as Stotz, Altschull and Hogness (12) have recently shown, the cytochrome must also be

combined with the oxidase. Thus, the mediation of the reaction between reduced cytochrome and molecular oxygen requires the simultaneous combination of *both* substances with the oxidase.

A similar relationship is apparent in the yellow enzyme respiratory system:

$$\text{Metabolite } (DH_2) \xrightarrow{\text{dehydrogenase}} \text{Coenzyme } (Co) \rightleftharpoons$$

$$\text{Flavoprotein } (FP) \longleftarrow \text{Oxygen}$$

or:

$$DH_2 + Co \rightarrow D + CoH_2$$
$$CoH_2 + FP \rightarrow Co + FPH_2$$
$$FPH_2 + \tfrac{1}{2}O_2 \rightarrow FP + H_2O$$

Here the oxido-reduction reaction between the metabolite and the coenzyme (a reversible oxidizable pyridine nucleotide) is mediated by the dehydrogenase. This enzyme is, of course, a protein and in order to activate the metabolite must first bind it on its surface. In addition, as Warburg (13) has pointed out, the coenzyme must be simultaneously bound by the dehydrogenase protein. Here too, therefore, the transfer of hydrogen occurs only when both reactants are oriented on the surface of the enzyme protein.

The behavior of the flavoprotein is similar. This is an enzyme consisting of an alloxazine-adenine-dinucleotide prosthetic group and a specific protein "base". The prosthetic group is reversibly oxidizable, and its reaction with molecular oxygen depends on the binding of both substances by the protein moiety. Usually the enzyme is thought of as consisting of both the protein and prosthetic group, and only such substances as the metabolite or oxygen given the status of "substrate." Actually, however, both the prosthetic group and oxygen act as substrates of the flavoprotein, while both the coenzyme and metabolite are joint substrates of the dehydrogenase.

It is clear that the ordering of the individual oxido-reductions which make up the cellular respiratory systems is accomplished through the spatial orientation of the various reactants by the appropriate enzymes. Thus, the fact that the metabolite is oxidized by the coenzyme, rather than reacting with some other substance, is due to the joint binding of metabolite and coenzyme by the dehydrogenase. In a similar way the reaction between oxygen and reduced flavin is determined by the combination of both substances by the same protein. When we further recall that all such combinations must occur at specific points on the protein, it is obvious that the paths of these reactions are determined by the structural properties of the enzyme proteins.

Such *in vitro* systems still retain a certain degree of chemical freedom. The path of the reactions is clearly due to the enforcement by the proteins of a fixed orientation of the various reactants. At only one point in the system is this structural rigidity lacking. This appears in the yellow enzyme system, for example, in the hydrogen transfer by diffusion of the coenzyme between the dehydrogenase and the flavoprotein. This diffusibility, which certainly occurs in such *in-vitro* systems, could permit of certain alterations in the path of reaction—such as reaction of the coenzyme with some other diffusible carrier. However, the main sequential features are determined by the structural properties of the enzymes, and we shall see below that even the small degree of freedom that does occur *in-vitro* is greatly restricted in the cell.

STRUCTURE WITHIN THE LIVING CELL

The foregoing discussion has been restricted to the structural properties of respiratory enzyme systems *in-vitro*. All of the structural restrictions which appear *in-vitro* also hold within the cell, but the normal integrity of the protoplasm must clearly introduce new restrictions which are peculiar to it.

The basis of the relationship between the respiratory activity of the intact cell and the structural properties of the cell protoplasm is, therefore, a problem of the first magnitude. It is, however, unfortunately true that the available data are as yet very inadequate, and any attempt to elucidate the problem must perforce be distinctly tentative.

Three lines of approach suggest themselves: (1) an examination of the chemical behavior of intact cells in order to reveal the nature of the sequential rigidity of the respiratory systems; (2) a study of the effect of natural and induced intracellular structural changes on the characteristics of the respiratory systems; (3) direct observation of the actual molecular architecture of the cell and the description of its relation to changes in enzyme activity. All three approaches are equally important to the solution of the problems of intracellular organization and it may be worth while to examine each of them in greater detail, again using respiration as a general example of enzyme activity.

Structural orientation as expressed in the respiratory activities of intact cells

We have already seen that the chemical properties of the systems discussed above are closely dependent upon the structural orientation of the reactants. Now, if the organizational characteristics of living protoplasm impose new structural restrictions on the chemical processes which it carries out, then some evidence of this should be apparent in the chemical data obtained from intact cells.

That this evidence exists can be seen at once from the fact that the cell's respiratory activity is not carried out by a single system. If all the various oxido-reduction reactions which may take place in the cell were in direct molecular communication one with another, we would then expect the transfer of hydrogen between oxygen and the metabolite, to travel a continuous and uninterrupted path from one reaction to the other. The E_0 values of the various reactions should indicate which linkages are possible, and if this freedom of contact existed, there would automatically be constituted an unbroken chain of H transport, each reaction assuming the place (in the series) dictated by its E_0 value.

In such a (hypothetical) system, the rates of the separate reactions would determine the relative activity of the various branches and shunts in the chain, but the whole sequence would be in a continuous kinetic equilibrium. This indicates a second consequence of such homogeneity: the blocking of one link in the chain (eg. by a poison) should result in the shunting of H transport to other branches of the series, and the reestablishment of equilibrium within the chain. Thus the blocking of O_2 consumption by one part of the system would be expected to result in greater respiratory activity of other parts.

This hypothesis does not meet the test of the *in-vivo* data. The data show that cell respiration is not carried out by a single continuous system. Rather, as we shall see below, the oxido-reduction reactions in the cell have a very restricted course of activity. The various reactions are not in equilibrium with each other, but operate in a strikingly discontinuous manner. The respiratory sequence is not determined by the *possibility* of reaction but by the structural orientation which forces or prevents specific molecular collisions.

An example of this type of evidence is offered by the data on the cyanide-sensitivity of cell respiration (see Commoner (14)). Cyanide, even in maximal concentration, will inhibit only a part of the respiratory activity of most cells. Since cyanide has been shown to be a specific poison for the cytochrome oxidase, this at once indicates that part of the oxygen consumption is not mediated via this enzyme. Further, it can be shown that the cyanide-stable respiration (which is probably due to the activity of a flavo-protein capable of reaction with molecular oxygen) accounts for a small but constant amount of oxygen consumption, while the oxygen utilized via the cyanide-sensitive system is much larger and more variable in magnitude. Changes in respiratory rate which occur during various cytological events such as fertilization of eggs and germination of spores, are accountable by variation in the rate of activity of the cyanide-sensitive system alone. The cyanide-sensitive system appears to use carbohydrates and similar substances, while the insensitive system tends to oxidize proteins and fats. Thus, if glucose is added to a suspension of *Chlorella* cells for example, the rate of oxygen consumption rises sharply, but the amount of cyanide-stable respiration remains constant. If there were a kinetic link between the two systems we would expect the blocking of the cytochrome oxidase by cyanide to result in an increased activity of the insensitive system. In addition it would be expected that the increased respiration due to the addition of substrate would be shared by the two systems. Neither of these effects occur, and it must be concluded that such a kinetic link is lacking. The two systems appear to be distinctly separate mechanisms of oxygen consumption, and it is clear that the constituent oxido-reduction reactions must be rigidly ordered and not subject to free interaction. That this rigidity is a function of the intracellular structure is borne out by the fact that the separation between the two systems disappears when the cellular integrity is disrupted. Thus, Ogston and Green (15, 16) find that the oxidation of hexose phosphate by intact yeast cells is cyanide-sensitive, but its oxidation by a system "reconstructed" from extracts of the same cell is cyanide-stable.

Further evidence of this sort can be found in examining the relationship between respiration and various other cellular functions. Thus, it is found that most changes in respiratory rate during embryogeny occur solely within the cyanide-sensitive system. The variation in respiration between

BOSTON UNIVERSITY
COLLEGE OF LIBERAL ARTS
LIBRARY

different species of bacteria and different organs of animals and plants is due to differences in cyanide-sensitive respiration alone. The increased oxygen consumption of muscle and of various glandular tissues incident to their activation, is entirely cyanide-sensitive. Hence, the respiratory dependence of these functions is restricted to a particular part of the total respiratory apparatus of the cell, and again a kinetic equilibrium between the various parts is precluded.

A similar relationship obtains between growth and respiration in plants. Commoner and Thimann (17) have shown that in the *Avena* coleoptile, the effectiveness of auxin as a growth hormone is related to its activation of a specific and small part of the total respiratory system (the four-carbon dicarboxylic acids). The respiratory activity of the four-carbon acids (which are H carriers) is necessary for *all* of growth, but is responsible for but a *small* part of the total respiration; and when it is blocked, growth ceases entirely while the rate of respiration falls but 10 per cent. Again, there is a specific orientation of the component parts of the respiratory system.

Similarly, the data of Fisher (18) and Clowes and Krahl (19) suggest that reproduction of yeast cells is connected with a discrete portion of the cell's respiratory system.

These cases point to the existence of a rigid specificity between the energy producing respiratory processes and the various endothermic functions which utilize the energy thus produced. The energy produced by cellular oxidation cannot be thought of in terms of a pooled fund which is merely apportioned to various endothermic processes according to need. Rather, the union between the two types of process seems to be due to a specific orientation between the two reactions concerned.

The relations of the separate reactions *within* a given respiratory chain seem to follow the same pattern of discontinuity. This has been pointed out for the case of the Warburg-Keilin system by Commoner (14). The activity of the Warburg-Keilin system depends on two *external* factors: the concentrations of molecular oxygen and of the metabolite substrate. The metabolite is activated by its specific dehydrogenase and the rate of dehydrogenation will vary with the metabolite concentration according to the usual hyperbolic function. The same is true of the relationship between pO_2 and oxidase activity, but in this case the enzyme activity may also be reduced by using greater or lesser amounts of cyanide. Thus, by measuring the rate of respiration of bakers' yeast in various concentrations of dextrose and cyanide it was possible to study the relation between the rate of oxygen consumption and the activity of the oxidase and the dehydrogenase.

If these enzymes were in a kinetic equilibrium we would expect the respiratory rate to be some function of the *product* of the two rates of activity. This, however, does not occur. In low sugar concentrations when the dehydrogenase is relatively inactive, the rate of respiration is not affected by cyanide concentrations which reduce the oxygen consumption of sugar-saturated cells. That is, when the dehydrogenase activity is low, part of the oxidase activity can be negated without affecting the rate of respiration. The inverse relation also holds, for when the oxidase activity is low (in the presence of cyanide), then the rate of respiration is not affected by the addition of dextrose in amounts which would increase the oxygen consumption of unpoisoned cells considerably. This type of kinetic discontinuity has been observed in a number of similar cases (see Commoner (14)).

In the data cited above, we can see a clear reflection of the heterogeneity inherent in the enzymatic catalysis of chemical activities. In the cell itself, the separate reactions that constitute the enormously complicated network of metabolic systems, are rigidly linked in a specific order. The transport of hydrogen is mediated by well-defined and distinctly separate paths, each of which seems to act in a more or less autonomic fashion. The thermodynamic characteristics of the separate reactions are but *permissive* properties; the actual exercise of these potentialities is very limited since the ordering of the respiratory sequence seems to permit few alternative paths of hydrogen transport.

It can be seen that homogeneous kinetic links are almost non-existent in the cellular metabolic apparatus. The separate enzymes, besides having their own internal structural properties, must be held in a fixed orientation relative to each other. There seems to be little or no evidence of homogeneous, "dilute solution" kinetics in the cellular respiratory systems. It must be concluded that the cellular protoplasm is characterized by an inter-enzyme structure which plays the predominant rôle in determining the course of chemical events in the cell.

The effects of changes in intracellular structure on respiratory activity

It is obvious that the mechanical destruction of a cell has a serious effect on its biochemical properties if only because of the fact that disintegration inevitably follows. The effect on respiratory activity is especially marked. Even such a relatively slight mechanical disorientation as mincing has a drastic influence on the respiratory metabolism of most tissues. Intact tissues will deaminate l-amino acids, but minced tissues will not do so (Krebs(9)). Mincing destroys the capacity of liver tissues to metabolize fatty acids. The mincing of muscle results in a 4- to 6-fold increase in the rate of respiration and a shift of the respiratory quotient from 0.8 to 1.0. That is, mincing brings into play a rapid oxidation of the carbohydrate contained in the muscle (Schorr and Barker (21)). Kostychev has shown that the abrasion of plant tissues increases the rate of respiration and proteolysis. Even the mere bending of a leaf will induce a sharp rise in the rate of respiration (Audas (22)). The literature contains many examples of this kind.

Cytolysis has a similar effect on respiration. The classical work of Warburg (2) although perhaps now overshadowed by his more recent researches is clearly illustrative of this fact. When erythrocytes were cytolyzed the rate of respiration fell off sharply. If the cell masses were then centrifuged, the supernatant "structureless" (i.e. liquid) fraction had almost no oxygen consumption while the heavier "structural" precipitate contained all of the respiratory activity of the cytolysate. However, if the latter material was ground up with sand, all of the respiration vanished. Cytolysis of sea-urchin eggs gave similar results, the further significance of which will be discussed below.

That such quantitative effects of cytolysis are based on qualitative disorientation of the respiratory system is apparent in certain more recent researches. Penrose and Quastel (23) found that lysis of *Micrococcus lysodeikticus* results in a 90 per cent reduction in respiration rate. However, while the activity of the dehydrogenases was largely destroyed. the activity of the cytochrome oxidase, catalase and fumarase *increased* slightly. In some cases, cytolysis increases the rate of respiration, as in amphibian embryos (Brachet (24)), or in the well-known effect of wounding in plant tissues. Specific activities which are related to cell respiration, such as bacterial luminescence depend on the integrity of the cellular structure (Korr (4)).

It is not surprising therefore, that the characteristics of extracted respiratory systems are often far from similar to those of the system *in-vivo*. Thus, the systematic researches of Ogston and Green (15, 16) on the properties of "reconstructed" enzyme systems reveal that the yellow enzyme system will carry out many oxidations *in-vitro* which it does not mediate in the living cell.

Changes in intracellular structure that occur during the normal life of a cell are also accompanied by such changes in respiratory activity. A case in point is the fertilization of eggs. Almost at the instant at which the sperm penetrates the egg membrane (in the marine eggs at least) a violent churning and streaming begins to agitate the protoplasm, new membranes are elevated from the egg's surface, and embryonic development begins. Such changes must obviously have some effect on the intracellular structure and it is not surprising to find that they are accompanied by sharp changes in respiratory activity. It was first observed by Warburg (25) that fertilization of sea-urchin eggs causes a sudden rise in the rate of respiration. Later investigations by other workers showed that the increase was of the order of 5–7 times, and that it occurred within one minute after fertilization.

Most marine eggs exhibit some change in respiratory rate at fertilization. A summary of these effects by Whitaker (26) shows that the direction of the change of rate depends on the rate of the unfertilized egg. If the respiration of the unfertilized egg is low, then it rises upon fertilization (as in *Arbacia*), but if the absolute rate is at first high, it falls when the egg is fertilized (as in *Chaetopterus*). The absolute rates of various fertilized eggs tend to be very similar in value, fertilization seeming to bring the rate to this general level regardless of its value in the unfertilized egg. It would appear from this that the effect of the activity within the cell at fertilization is to release the unfertilized egg from its stable state by reorienting the enzyme relations in the respiratory system.

That this effect also entails a qualitative change in respiratory activity is shown by the work of Runnstrom (27) and Korr (28) on *Arbacia* eggs. Both demonstrate that the increase in respiratory rate at fertilization is due to the sudden activation of the Warburg-Keilin system. Recently, Ballentine (29) has shown that this activation is ac-

complished by an increase in the activity of the dehydrogenases. He has also found that, in the case of *Chaetopterus*, when the rate falls upon fertilization there is a corresponding decrease in dehydrogenase activity.

Later stages in embryogeny show similar respiratory phenomena. Thus, during the diapause in development of Orthoptera, when all developmental activity temporarily halts, the respiration falls to a low value and is completely accountable by a system which is not affected by cyanide. During the active stages in development, however the rate is much higher, and this increase in respiration is due solely to the increased activity of the Warburg-Keilin system. (Bodine and Boell (30)).

Goddard and Smith (31) have shown that the activation and germination of dormant spores of *Neurospora* is accompanied by a forty-fold increase in the rate of respiration. This increase is due to the suddent activation of the Warburg-Keilin system. Similarly the excystment of *Colpoda* from resting cysts, which involves violent intracellular activity and the complete differentiation of the trophic form within one hour after activation, is accompanied by a sharp rise in the rate of respiration (Commoner (32)).

There is little doubt that the stuctural alteration of the protoplasm produces profound changes in the orientation of the oxidative processes which it mediates. The data cited above but reinforce the conclusion reached on the basis of the sequential properties of the metabolic processes (section 1): The enzymes in the living cell are inter-related in such a manner as to constitute a relatively rigid structure which limits and orients the chemical activities which they carry out.

The next problem which must be faced is the basis of this structural organization.

The molecular basis of intracellular structure

So far, our discussion of intracellular structure has been based on relatively circumstantial evidence. This approach is a necessary and important one, but at the same time must be accompanied by a direct attack on the actual molecular arrangements in the cell and their relation to the chemical rigidity which characterizes respiration in the cell. Very little evidence of this kind is on hand as yet, and the present examination of the problem must perforce be but tentative and suggestive.

The problem of the physical nature of protoplasm has been the subject of extensive research. The older workers, emphasizing the fluidity of protoplasm, have looked upon it as an emulsion of two liquid phases, the one aqueous and the other fatty, with various constituent substances dissolved in each phase. Thus, according to Bayliss (33) "protoplasm behaves as a liquid". On the other hand, the regulated complexity of the chemical behavior of living protoplasm gave rise to a hypothesis of a more rigid cellular structure. This is exemplified in Hofmeister's concept of the cell as a complex of separate "chemical laboratories". In addition the apparent spontaneity and physical autonomy of protoplasmic processes led other workers, such as Pflüger and Verworn to postulate a special kind of living molecule, the biogen, which either constituted the entire cell or served as the "living spark" that activated the "inert" parts of the cell.

Subsequent advance in analytical biochemistry has tended to repudiate this type of concept. Protoplasm was found to contain a huge melange of proteins, carbohydrates, fats, and numerous other kinds of organic and inorganic substances. It seemed absurd to place the burden of protoplasmic "vitality" upon any one of these many constituents.

With the new knowledge that all cellular chemical activities are mediated by enzymes, that all enzymes contain protein moieties, and that the enzymes are structurally inter-related, it is possible, indeed necessary, to re-assess the significance of the protoplasmic constituents. If it is correct to conclude that the organization of metabolic processes and the maintenance of the complicated chemical systems that characterize living protoplasm is accomplished through enzyme inter-relations, then we must look upon the cell's protein constituents in a new light. It would appear that in the proteins can be found the basis of the orientation of metabolic activities, and that the other constituents, however important, must be considered in terms of their relation to the enzymes of the cell. This conclusion is amplified if we further note, that of all cell constituents there is none which possesses the enormous structural potentialities of the long carbon chains and interacting side-chains of the protein molecule. This organizational rôle of the cell protein is borne out by a number of direct experiments.

The early work of Batelli and Stern (3) gave rise

to the concept of two kinds of cell respiration: the "main respiration", which was associated with the intact structure of the cell, and the "accessory respiration" which was a property of the fluid constituents. Warburg (34) found that the granules sedimented (by centrifuging) from ground liver suspension contained 20 per cent of the tissue respiration, while the supernatant fluid contained but 4 per cent. Banga (35) working with pigeon breast muscle suspensions, found that the centrifuged sediment consisted of small granules which contained cytochrome, cytochrome oxidase, succinic, malic, and citric dehydrogenases. However, these granules showed very little oxygen consumption unless the supernatant (which itself had almost no oxygen uptake) was also present. The suspension was therefore presumed to contain soluble coenzymes. More detailed work of this kind carried out by Greville (36) also indicated that both the sediment and supernatant are required for maximum respiration, and it was also shown that in no case did the oxygen consumption persist for longer than some 200 minutes. More recently Stern (37) has shown that the granules (obtained from heart muscle) are apparently spherical macromolecules of a molecular weight of some hundreds of millions. The granules are mainly protein but also contain lipoids, nucleic acid and hemin. Stern also finds the respiratory activity to be of a very short duration.

A similar material has been found by Kabat and Furth (38) and by Claude (39) in a wide variety of normal and malignant tissues. Kabat and Furth have shown that the filterable virus which induces chicken leukemia and sarcoma is associated with a protein particle of the same huge size. Furth and Kabat (40) have also found that the Forssman antigen which occurs in a great variety of species is also associated with this protein fraction in tissue extracts. It is interesting to note that this large protein body often contains as much as 20 per cent of the total N content of cell extracts.

It seems clear that we are here dealing with a very common protein particle which contains a number of enzymes and other active proteins and may carry out, for a short time, oxidative activities in the presence of soluble cell extracts or the proper coenzymes. Stern (41) suggests that this particle contains all the "fixed" enzymes of cell respiration and states: "We consider our particles as 'subcellular' functional units and we believe that the active groups of the various component catalysts are arranged in or on them in an orderly fashion so as to ensure a smooth functioning of the highly complex process of cell respiration." It is also suggested that the respiratory chain is constructed from the enzymes fixed in this particle and the diffusible carriers which link them. (See also Euler and Adler (42), and Dewan and Green (43).)

Do such particles really exist as independent "functional units" within the cell? In the first place it seems clear that these granules, even together with the accessory diffusible coenzymes, do not constitute the entire integrated system of cell respiration, since in no case do such *in-vitro* systems consume oxygen for a period longer than two or three hours. Furthermore, from the evidence cited in the previous sections we must conclude that the relationship between the enzymes "fixed" in the macromolecules, and the carriers which are "freely diffusible" is a rather rigid one. It hardly seems valid to postulate that either part of the respiratory mechanism exists as a structurally free unit within the cell.

The structural rigidity of the position of these macromolecules within the cell is emphasized by the data obtained with the high speed ultra-centrifuge. Particles of such a size should be sedimentable in the ultra centrifuge, but Beams and King (44) find that on the ultra centrifugation of *Ascaris* eggs "No evidence was found which indicates a separation of the ultra-microscopic cytoplasmic components had taken place". Bodine and Boell (45) find that ultra-centrifugation does not affect the rate of respiration of grasshopper eggs in the diapause condition. However, actively developing eggs, which have a much higher normal respiration (which is cyanide-sensitive) suffer a forty per cent reduction in rate. It seems likely that the explanation of this effect and of a similar case in *Arbacia* (Shapiro (48)) is that the large amount of substrate required for the maintenance of high rates of respiration may be in part segregated from the proper enzymes. There does not seem to be any fundamental disorientation of the enzyme system in these cases.

Although the data on this point are still very limited, it seems likely that the enzyme-bearing macromolecules, which can be sedimented *in extracts*, maintain a fixed position when subject to the same gravitational forces *within the cell*. It would seem, then, that this protein, which contains an appreciable amount of the total N in the cell, pervades the entire protoplasm and cannot be

separated from the normal integral structure of the cell. Thus, the enzymes which are associated with this material must also be structurally oriented throughout the cell. Such a structure is reminiscent of the "cytoskeleton" suggested on theoretical grounds by Peters (47) and Needham (48); its relation to cell respiration has been more recently discussed by Korr (6). Such a structure appears to be the organizing medium for the complicated chemistry of cellular metabolism.

It becomes apparent, then, that the enzymes within the cell are under structural restrictions even greater than those characteristic of serial enzyme processes *in-vitro*. Reference above will show that the sequential properties of the yellow enzyme system (for example) *in-vitro* are due to the *internal* structural properties of the two proteins which are involved, both being free to move about in the solution. This freedom, which makes possible the occurrence of oxidative reactions which this system does *not* mediate in the cell is lacking in protoplasm itself.

In the living cell the enzymes seem to be linked together through their mutual association with the heavy protein constituents that pervade the cell. Under these circumstances diffusible hydrogen carriers, such as the coenzymes, appear to be captive within certain parts of the inter-enzyme structure and so serve to further the chemical rigidification of the *in-vivo* respiratory systems. The protein structure within the cell is the organizer of cellular metabolism.

CONCLUSIONS

We have here been concerned with the effect of the structural orientation of cellular oxidative enzymes upon the respiratory activity which they mediate. It seems clear that the ordering of the complex of respiratory processes is dependent on enzyme and inter-enzyme structure.

The importance of this problem is obvious from the breadth of the effects which are included in its scope. The most serious factor limiting the further development of such studies is the need for new experimental approaches and techniques. Three methods of attack were mentioned in the preceding section and it is perhaps appropriate to conclude by suggesting certain new possibilities.

Thus far we have been dealing, in the main, with enzyme systems as already constructed within the cell. In actuality, of course, the respiratory enzyme systems are subject to many developmental changes. Some of these have been mentioned above as examples of enzymatic reorganizations which accompany structural activations such as fertilization and germination. However, it may also be suggested that such cases of enzyme development may offer opportunities for the study of the structural properties of the respiratory systems which ensue. This could be done, for example, by studying the effect of environmental conditions on the properties of the enzyme systems during the process of development.

Enzyme activation and formation is a very widespread phenomenon and is affected by a number of environmental conditions. Thus Ashford and Dixon (49) show that the K/Ca balance controls the availability of the respiratory enzymes in brain tissue. Similarly Iljin (50) finds that the K, Na/Ca ratio regulates the activity of amylase in leaves. It is possible that this type of effect can be correlated with the known effects of salt balance on protein structure.

What is perhaps a more important influence on enzyme structure is exerted by the substrates themselves. Enzymes can often be produced by introducing the specific substrates to the organism's environment. Such enzyme adaptation or "training" has been found particularly among the bacteria (see the recent review of Dubos (51)). If a bacterium which is normally incapable of oxidizing a particular substrate is cultured in a medium containing this substance, there is often produced, in the course of one or two transfers, the enzyme capable of acting on it. When the substrate is removed the new adaptive enzyme quickly disappears. Thus, the make-up of the respiratory system may be rapidly altered merely by the presence of a new metabolite. Such effects may permit us to study the conditions governing the development of enzyme systems and so to further elucidate their structural organization.

There are, undoubtedly, many such avenues of attack on the relation between cellular metabolism and intracellular structure. There is a clear need for further attention along these lines.

The continued development of our knowledge of cellular respiratory systems, which has in the past been so greatly advanced by analytical biochemistry, now appears to require more than the mere analysis of extracted enzymes. It requires more than the reconstruction of hypothetical systems from the analytical data. In fact, the very accumulation of such data has itself forced

upon us the conclusion that the most important factor determining the course of chemical events in the cell is the very structure which is destroyed in the process of extraction. The old type of analytical biochemistry has itself pointed the way to a new approach.

It is perhaps useful to remind ourselves of Claude Bernard's characterization of theories: "they are only partial and provisional truths which are necessary to us, as steps upon which we rest, so as to go on with investigation; they embody only the present state of knowledge, and consequently they must change with the growth of science" (52).

LIST OF LITERATURE

(1) GREEN, D. E. 1937. Reconstruction of the Chemical Events in Living Cells. *In* Perspectives in Biochemistry. (Edited by J. Needham and D. E. Green), pp. 175–186. *Cambridge* (Cambridge University Press).

(2) WARBURG, O. 1913. Struktur und chemische Vorgange im Zelle. Thesis. *Heidelberg.*

(3) BATELLI, F., and L. STERN 1907. Action de quelques substances sur l'activité respiratoire des tissus isoles. *Jour. Physiol. Path. gen.*, 9, pp. 228–248.

(4) KORR, I. M. 1935. The relation between cell integrity and bacterial luminescence. *Biol. Bull.*, 68, 347–354.

(5) STIER, T. J. B., and M. I. NEWTON 1939. Changes in the rate of respiration of bakers' yeast during assimilation. *Jour. Cell. Comp. Physiol.*, 13, 345–351.

(6) KORR, I. M. 1939. Oxidation-reductions in heterogeneous systems. *Cold Spring Harbor Symposium*, 7, 74–93.

(7) HALDANE, J. B. S. 1930. Enzymes. *London* (Longmans, Green and Co.).

(8) QUASTEL, J. H. 1926. A theory of the mechanism of oxidations and reductions *in vivo*. *Biochem. Jour.*, 20, 166–194.

(9) KREBS, H. A. 1935. Deamination of amino acids. *Biochem. Jour.*, 29, 1620–1644.

(10) KUHN, R., and F. BAR 1934. Zum photochemischen Verhalten des Lactoflavins; Modell-Versuche in der Chinoxalin-Reihe. *Ber. Deutsch. Chem. Ges.*, 67, 898–904.

(11) KORR, I. M. 1938. Oxidation-reduction potentials in heterogeneous systems. *Jour. Cell. Comp. Physiol.*, 11, 233–245.

(12) STOTZ, E., A. M. ALTSCHUL and T. R. HOGNESS. 1938. The cytochrome C-cytochrome oxidase complex. *Jour. Biol. Chem.*, 124, 745–754.

(13) WARBURG, O. 1938. Chemische Konstitution von Fermenten. *Ergeb. Enzymf.*, 7, 210–245.

(14) COMMONER, B. 1940. Cyanide inhibition as a means of elucidating the mechanisms of cellular respiration. *Biol. Rev.*, 15, 168–201.

(15) OGSTON, F., and D. E. GREEN 1935. The mechanism of the reaction of substrates with molecular oxygen. I. *Biochem. Jour.*, 29, 1983–2004.

(16) ——, and —— 1935. The mechanism of the reaction of substrates with molecular oxygen. II. *Biochem. Jour.*, 29, 2005–2012.

(17) COMMONER, B., and K. V. THIMANN 1941. On the relation between growth and respiration in the Avena coleoptile. *Jour. Gen. Physiol.*, 24, 279–296.

(18) FISHER, K. C. 1940. Urethane and the respiration of yeast cells. *Collecting Net*, 15, 65.

(19) CLOWES, G. H. A., and M. E. KRAHL 1936. Studies on cell metabolism and cell division. I. On the relation between molecular structures, chemical properties, and biological activities of the nitrophenols. *Jour. Gen. Physiol.*, 20, 145–171.

(20) COMMONER, B. 1939. The effect of cyanide on the respiration of baker's yeast in various concentrations of dextrose. *J. Cell. and Comp. Physiol.*, 13, 121–138.

(21) SCHORR, E., and S. B. BARKER 1939. *In vitro* action of insulin on minced avian and mammalian muscle. *Biochem. Jour.*, 33, 1798–1809.

(22) AUDUS, J. L. 1939. Mechanical stimulation and respiration in the green leaf. II. Investigations on a number of angiospermic species. *New Phytol.*, 38, 284–288.

(23) PENROSE, M., and J. H. QUASTEL 1930. Cell structure and cell activity. *Proc. Roy. Soc.* (B), 107, 168–181.

(24) BRACHET, J. 1934. Étude du metabolisme de l'oeuf de grenouille (*Rana fusca*) au cours du développement. *Arch. de Biol.*, 45, 611–727.

(25) WARBURG, O. 1908. Beobachtungen über die oxidations Prozesse im Seeigelei. *Zeit. Physiol. Chem.*, 57, 1–16.

(26) WHITAKER, D. M. 1933. On the rate of oxygen consumption by fertilized and unfertilized eggs. V. Comparisons and interpretation. *Jour. Gen. Physiol.*, 16, 497–528.

(27) RUNNSTROM, J. 1930. Atmungmechanismus und Entwicklungserregung bei dem Seeigelei. *Protoplasma*, 10, 106–173.

(28) KORR, I. M. 1937. Respiratory mechanisms in the unfertilized and fertilized sea urchin egg. A temperature analysis. *J. Cell and Comp. Physiol.*, 10, 461–485.

(29) BALLENTINE, R. 1940. Analysis of the changes in respiratory activity accompanying the fertilization of eggs. *J. Cell. Comp. Physiol.*, 15, 217–332.

(30) BODINE, J. H., and E. J. BOELL 1934. Respiratory mechanisms of normally developing and blocked embryonic cells (Orthoptera). *Jour. Cell. Comp. Physiol.*, 6, 97–113.

(31) GODDARD, D. R., and P. E. SMITH 1940. Respiratory block in the dormant spores of *Neurospora tetrasperma*. *Plant Physiol.*, 13, 241–264.

(32) COMMONER, B. 1940. (Unpublished.)

(33) BAYLISS, W. M. 1927. Principles of General Physiology. Fourth Edition. *London* (Longmans, Green and Co.).

(34) WARBURG, O. 1913. Über sauerstoffatmende Körnchen aus Leberzellen und über Sauerstoffatmung in Berkefeld-Filtraten wassriger Leberextrate. *Pfluger's Arch.*, 154, 599–617.

(35) BANGA, I. 1937. Über den Aktivator und Donator der Hauptatmung des Taubenbrustmuskels. *Zeit. Physiol. Chem.*, 249, 183–188.

(36) GREVILLE, G. D. 1937. Fumarate and tissue respiration II: The respiration of pigeon breast muscle dispersions. *Biochem. Jour.*, 31, 2274–2286.

(37) STERN, K. G. 1940. Biological oxidations and reductions. *Ann. Rev. Biochem.*, 9, 1–42.

(38) KABAT, E. A., and J. FURTH 1940. Chemical and immunological studies on the agent producing leukosis and sarcoma of fowls. *Jour. Exper. Med.*, 71, 55–70.

(39) CLAUDE, A. 1937. Fractionation of chicken tumor extracts by high speed centrifugation. *Amer. Jour. Cancer*, 30, 742–748.

(40) FURTH, J., and E. A. KABAT 1940. Association of the heterogenic antigen with a material in normal and tumor tissues sedimentable at high speeds. *Science*, 91, 483–485.

(41) STERN, K. G. 1939. Respiratory catalysts in heart muscle. *Cold Spring Harbor Symposium*, 7, 312–322.

(42) EULER, H. VON, and E. ADLER 1937. Co-Zymase das wasserstoffübertragende Co-Enzym bei der Muskel-Glycolyse. *Zeit. Physiol. Chem.*, 245, 217–245.

(43) GREEN, D. E., and J. G. DEWAN 1937. The reversible oxidation and reduction of co-enzyme, I. *Biochem. Jour.*, 31, 1069–1073.

(44) BEAMS, H. W., and R. L. KING 1937. The suppression of cleavage in *Ascaris* eggs by ultracentrifuging. *Biol. Bull.*, 73, 99–111.

(45) BODINE, J. H., and E. J. BOELL 1936. The effect of ultracentrifuging on the respiratory activity of developing and blocked embryonic cells (Orthoptera). *Jour. Cell. Comp. Physiol.*, 7, 455–463.

(46) SHAPIRO, H. 1935. The respiration of fragments obtained by centrifuging the egg of the sea urchin, *Arbacia punctulata*. *Jour. Cell. Comp. Physiol.*, 6, 101–116.

(47) PETERS, H. 1938. Proteins and Cell Organization. *In* Perspectives in Biochemistry (Edited by J. Needham and D. E. Green), pp. 36–44, *Cambridge* (Cambridge Univ. Press).

(48) NEEDHAM, J. 1937. Order and Life. *New Haven* (Yale University Press).

(49) ASHFORD, C. A., and M. DIXON 1935. The effect of potassium on the glucolysis of brain tissue with reference to the Pasteur effect. *Biochem. Jour.*, 29, 157–168.

(50) ILJIN, W. S. 1938. *Quoted* in Oparin, The Origin of Life. *New York* (The Macmillan Co.).

(51) DUBOS, R. J. 1940. The adaptive production of enzymes by bacteria. *Bact. Rev.*, 4, 1–16.

(52) BERNARD, CLAUDE. 1865. Introduction à l'étude de la médecine expérimentale, *Paris*.

SUPERNUMERARY MAMMAE, WITH SPECIAL REFERENCE TO THE RHESUS MONKEY

By HAROLD SPEERT

Carnegie Institution of Washington, Department of Embryology, and Department of Obstetrics, Johns Hopkins Hospital, Baltimore, Maryland

SUPERNUMERARY breasts have been observed in the human with such frequency that little interest attaches at present to case reports of this condition, unless associated with unusual features. Deaver and McFarland collected 10,895 cases of supernumerary breasts from the literature in 1917 and de Cholnoky (1939) has recently added several more. From this vast material much information of statistical interest has been gained, and together with embryological studies, has helped dispel many of the misconceptions and superstitions which have permeated the subject. Studies of the occurrence of accessory nipples and mammary glands in other mammals have also been of great value in obtaining a truer interpretation of the biological significance of these anomalies. The object of the present paper is to examine the various views which have been held on the many interesting problems connected with the subject, and to report some observations on the occurrence and biological properties of supernumerary nipples and mammary glands in the rhesus monkey.

Interest in accessory mammae is manifested even in the art of the ancients, who occasionally endowed their goddesses with a number of breasts. The Phoenician goddess Astarte, for example, is said to have been frequently represented as having several mammary glands, and the statue of Diana of Ephesus, in the Vatican Museum in Rome, shows an extreme degree of polymastia, symbolic of fertility.

The early references to the subject plainly reveal the complete ignorance which existed concerning the significance of supernumerary breasts. One finds them referred to as *Teufelswerk, opus mirabile naturae ludentis,* and *une sorte de caprice ou de bizarrerie* (Hug, 1908). It is even stated (McGillicuddy, 1891) that Anne Boleyn was put to death by Henry VIII because she had a third breast.

ETIOLOGY

Concerning the etiology and mode of formation of supernumerary breasts several theories have been advanced; yet none is entirely capable of explaining all cases of polymastia.

1. Meckel von Hemsbach, in 1852, proposed the view that five was the original normal number of mammary anlages in the human; of these, one pair being situated in the pectoral region, one pair in the axillae, and the fifth in the midline at the base of the ensiform process. Ordinarily the superfluous glands underwent complete atrophy, but the occasional persistence of one or more of them he regarded as a satisfactory explanation for all the cases of ectopic mammae which came under his scrutiny. There was little if any evidence to support such a theory. It consequently attracted few adherents and soon fell into complete disregard.

2. Ahlfeld (1880) advanced the theory that polymastia was due to a splitting of the mammary anlage during embryonic life, and several years later Hansemann (1889) and Sutton (1889) expressed essentially the same idea. Ahlfeld also invoked the aid of the amnion in accounting for the location of the ectopic glands encountered. Their transplantation to various parts of the body surface was believed to have been brought about through the mechanical action of amniotic pressure and amniotic adhesions. Modern studies by Streeter, however, have demonstrated the inadequacy of amniotic adhesions in explaining the occurrence of various types of congenital abnormalities and have redirected attention from the mechanical action of the membranes to imperfections of the germ plasm.

3. Axillary swellings occur with relative frequency in puerperal women, and when associated with nipples or pores they often secrete a fluid

which is indistinguishable from milk. These tumors have generally been regarded as supernumerary mammary glands, but Champneys (1886), and later Seitz (1909), have regarded them as modified sweat glands which secrete milk under the appropriate hormonal stimulation of pregnancy and lactation.

4. Perhaps the most widely accepted interpretation of polymastia is that which regards this condition as a manifestation of atavism or of reversion. In the human, as well as in all other primates higher than lemurs, only one pair of mammary glands normally occurs. The lemur, however, possesses in addition to the pectoral glands a pair of inguinal "anchoring nipples," for the attachment of the young. Most species of sub-primate mammals possess a greater number of mammary glands, and in the insectivore *Centetes* eleven pairs are normally found.

Charles Darwin, from his study of comparative anatomy, and without the benefit of modern embryologic knowledge, came to the conclusion that polymastia in the human was a manifestation of reversion. In 1868, discussing this condition, he wrote as follows: "Many monstrosities can hardly be considered as the result of an arrest in development; for parts of which no trace can be detected in the embryo, but which occur in other members of the same class of animals or plants occasionally appear, and these may probably with truth be attributed to reversion," and in a later sentence he expresses himself as having been led "to the belief that in all cases the additional mammae in woman are due to reversion." In his Descent of Man, however, published several years later (1871), he finds it difficult to explain the occasional occurrence of mammae erraticae on the back, thigh, or in the armpit, and admits that "the force of my argument is greatly weakened or perhaps quite destroyed."

A knowledge of the embryonic development of the mammary gland is indispensable to an understanding of more recent interpretations of the significance of polymastia. In the human, as in all other mammalian forms that have been studied, the mammary apparatus is derived from a paired epithelial thickening which runs longitudinally along the ventral surface of the embryo from the anterior to the posterior limb bud, and which is known as the Milchleiste (Schultze, 1892) or milk line. Hirschland (1898) has traced this structure even farther back and has found it to be derived in turn from another formation called the milk streak, which consists of a comparatively broad zone of the integument characterized by higher epithelium and by a condensation of the underlying mesenchyme. During the course of further development, localized elevations appear along the milk line, and the intervening portions disappear. Schultze (1892) has discussed the occurrence of the milk line in several mammalian species, and in addition to the "definitive Zitzen" which persist and represent the mammary anlages, he mentions the occurrence of "primitive Zitzen" which later disappear. Schmidt (1897) made essentially similar observations on human material and concurred with Schultze in the view that these structures represent supernumerary mammary anlages. Schultze therefore regarded polymastia as of ontogenetic as well as phylogenetic significance. Schmitt (1898) and Walter (1902), on the other hand, have questioned the interpretation that all such epithelial thickenings represent accessory mammary anlages. Nonetheless the view as enunciated by Wiedersheim (1908) came to be the generally accepted one, namely, that a condition of hyperthelia normally exists in the human embryo, and that occasionally, in addition to the main mammary anlages, one or more of the supernumeraries also undergo further development, thereby resulting in postnatal hyperthelia or hypermastia.

Leichtenstern (1878) and Neugebauer (1886) had already expressed their belief that polymastia was a manifestation of atavism, and upon the basis of the detailed embryologic studies mentioned, this view was soon subscribed to by Bonnet (1892), Kayser (1908), Bresslau (1909), and others.

5. Accessory mammary glands or nipples occurring in the vicinity of the primitive milk lines are perhaps adequately explained by the latter theory. Axillary, thoracic, abdominal, inguinal, and possibly vulvar mammae fall into this category. However, the literature contains numerous case reports, apparently well authenticated, of mammae erraticae occurring in bizarre locations such as on the face, ear, neck, arm, thigh, and buttock. No satisfactory explanation has been advanced for the development of these ectopic breasts, and they are simply referred to as sports or freaks of nature.

LOCATION, NUMBER, AND INCIDENCE

Although supernumerary mammary glands and nipples have been observed in many atypical posi-

tions (see reviews by Deaver and McFarland, and by de Cholnoky), the vast majority occur along the milk line, from the axilla to the groin, and most of them have been observed in the thoracic region. They may be unilateral or bilateral and may occur above or below the normal mammae. Von Bardeleben (1893) found among 8,568 young men with hyperthelia an incidence of thirty per cent of the supernumeraries occurring on the right side, thirty-nine per cent on the left side, and thirty-one per cent bilaterally. This is in general agreement with the findings of other authors (Leichtenstern, 1878; Bruce, 1879; Iwai, 1907a; Hathaway, 1909; and Landauer, 1939), who found a slight preponderance in favor of the left side.

When the extra nipple is situated above the normal one it is usually lateral to it, whereas when below it is medial. In general, as pointed out by Geoffroy Saint-Hilaire (1832), if a supernumerary gland is situated laterally it is well formed, of considerable size, and can lactate; if medial, it is usually small, imperfectly developed, and incapable of lactation. Most of the above authors have found the majority of the accessory mammae below the normally situated one, and Kajava *et al.* (1921), in their extensive study of a huge Finnish population, found 98.7 per cent of all accessory glands below the normal breasts. Iwai (1907a), however, in his examination of 511 Japanese polymastics, found eighty-eight per cent of the supernumerary breasts above the normal ones, thereby emphasizing the importance of the racial factor. He also found the incidence among females to be three times as great as among males, in contrast to the statistics of Leichtenstern, Bruce, Kajava *et al.*, and Landauer, which indicate a preponderance of supernumeraries among males.

Single accessories occur with the greatest frequency, and the incidence decreases inversely to the number of mammae. Graham-Campbell (1936) has reported the case of a patient with eight and possibly nine supernumerary nipples, and Neugebauer (1886) and Hirst (1912) described patients with eight and seven supernumerary breasts respectively, each of which secreted milk after childbirth.

Great variations exist among the statistical reports concerning the incidence of supernumerary nipples and mammary glands. Kajava *et al.* have reviewed the literature on the subject and have tabulated the incidences quoted by various authors, ranging from 0.05 per cent (Schwalbe) to 23.3 per cent (von Bardeleben). They themselves quote an incidence of 2.8 per cent for the Finnish population, as compared with an incidence of 3.75, quoted by Iwai for the Japanese. More recent estimates indicate that the true incidence is probably closer to one per cent. Tiffany (1906) has stated that the condition is more common among Negroes, and Stannus (1914) found fourteen cases among several native African tribes in Nyasaland. Although racial factors undoubtedly play an important rôle in explaining the apparent discrepancies, probably more importance should be attached to the different criteria used by the various observers in making the diagnosis of hyperthelia.

STRUCTURE

Kajava *et al.* (1921) classified supernumerary breasts into eight groups, depending upon the presence or absence of the nipple, areola, hairs, and mammary parenchyma. Twenty-six such breasts were subjected to histologic examination and were found to show all gradations from a structure barely suggestive of mammary tissue to that of a "typical" breast. Hoepfner (1899) had earlier examined nine male accessory nipples histologically and found a normal nipple structure, usually associated with only rudimentary mammary glandular tissue or sweat glands.

HEREDITARY ASPECTS; RELATION TO FECUNDITY AND TWINNING

It has long been realized that throughout the mammalian series the number of mammary glands characteristic of any species is, as a general rule, correlated with the average litter size of that species. This concept has been applied to the subject of polymastia in the human. In addition to its manifestation by the endowment of the goddesses of fertility with supernumerary breasts, the belief has become firmly established in scientific writings that fertility and twinning are associated with the occurrence of polymastia. Leichtenstern (1873) found three cases of twins among seventy patients with accessory mammaries, and Iwai (1907b) reported eighteen cases of multiple birth among 101 married women who had supernumerary glands. Although the total number of pregnancies is not stated, it is certain that the incidence of twinning in this group was larger than in the general population. The latter author also stated his belief that women with supernumerary mammary glands have a tendency to become pregnant

more frequently than others. Numerous case reports tend further to emphasize the relation between polymastia and multiple births. Marie (1893), for example, reported six pairs of twins in two generations of polymastics, and Pétrignani (1939) found six pairs of twins and a set of triplets in three generations of a family possessing this trait.

An experimental basis for this association was apparently established by the breeding experiments of Bell (1923), who succeeded in developing a flock of sheep with four or more nipples, and in which the ewes continued to bear twins or triplets every year, with hardly any single pregnancies. Bell's breeding data were later subjected to genetic analysis by Castle (1924) and by Ritzman (1933) and it was found that there was no necessary relation between nipple number and twinning. Geoffroy Saint-Hilaire (1832) and Flechsig (1840) had long before expressed their disbelief in any relation between polymastia and multiple births or fecundity, and recent writers have been of the opinion that the formerly held views were based upon inadequate statistics. More careful collection and evaluation of statistical data are needed before the problem can be considered settled.

The hereditary nature of supernumerary nipples and mammary glands has been subject to less controversy, for the familial occurrence of these anomalies has been generally recognized. Woodman (1868) reported a case of mother and daughter with third nipples in the same relative positions. Handyside (1873) described bilateral supernumeraries in brothers, and the present writer has found the same condition in father and son. Polymastia has also been reported in identical twins (Weitz, 1925; Birkenfeld, 1932). Cases illustrating the familial nature of supernumerary mammae have been observed with such frequency in recent years that the majority are of insufficient interest to warrent publication. Especially interesting is the report of Klinkerfuss (1924), who traced this condition through four generations of a family. Most famous, however, is the report by Marie (1893), in which is described the occurrence of supernumerary nipples in a young girl, all of her eleven siblings, her father, five paternal uncles, the grandmother, and the paternal great grandmother, a total of twenty cases in four generations.

RELATION TO TUBERCULOSIS

Claims for the association of polymastia with tuberculosis originated with the Japanese. Sato is said to have found nineteen cases of actual or suspected tuberculosis among twenty-nine individuals with polymastia, and the subject was investigated more extensively by Iwai. The latter author (1906, 1907c) found 4.97 per cent of 1930 tuberculous patients to have supernumerary breasts, as compared with an incidence of 2.71 per cent among 1514 non-tuberculous patients. Conversely, of ninety-six cases of polymastia, he found twenty-three per cent to be tuberculous, as contrasted with a tuberculosis incidence of ten per cent among non-polymastics. On the basis of these figures he maintained that cases of polymastia are found more frequently among the tuberculous, especially those with pulmonary tuberculosis, and that individuals with supernumerary breasts are more liable to be affected by tuberculosis than are others. Boenheim (1919) and Kajava *et al.* (1921) have been unable to confirm these associations among Caucasian races, and the claims of the Japanese authors have not received general acceptance.

RELATION TO LEFT-HANDEDNESS AND TO CONGENITAL ANOMALIES

The interesting observation has recently been made by Landauer (1939) that the incidence of left-handedness is higher among individuals with supernumerary nipples than among the general population. He found 145 of 709 cases of hyperthelia to be left-handed (twenty per cent), as compared with an incidence of eight per cent for this trait among the population at large. Stier (1912) had previously claimed that in left-handed individuals supernumerary areolae occur practically always on the left side, as contrasted with a right sided preponderance of supernumeraries among right-handed individuals.

Boenheim (1919) studied forty-eight cases of supernumerary nipples for manifestations of other anomalies and succeeded in demonstrating a high incidence of coincident abnormalities of various types. Malformations of the ears, he stated, were seldom absent, and skin anomalies (chloasmae, naevi, etc.) were common. Other coincident pathologic conditions which he recorded included imperfections of the eye (Horner's syndrome, abnormalities of the iris), high palate, various anomalies of the chin and teeth, gastric an- or hypo-acidity, *Tropfenherz*, epigastric hernias, and split ensiform processes.

CLINICAL ASPECTS

Supernumerary breasts are of interest chiefly from an academic standpoint. Nonetheless there are several conditions which demand consideration by the clinician. Perhaps the most common source of annoyance from accessory mammae is the pain which they cause during lactation. This is especially so if the gland is not equipped with an adequate outlet for its secretions. If a nipple and ducts are present, the dribbling of milk which frequently occurs may be quite bothersome to the patient. Cosmetic considerations are responsible for the formidable concern which many individuals manifest for the presence of supernumerary breasts, especially if they are large or if they occur in conspicuous or embarassing locations such as the face, neck, buttock, labia, etc.

Von Bardeleben (1891) suggested that accessory nipples and mammary glands are more prone to pathologic changes than are normal ones, and Williams (1895) reported a high incidence of neoplastic disease (fibroadenoma and carcinoma) in ectopic mammary tissue. Deaver and McFarland (1917) analyzed the reported cases of tumors arising in supernumerary breasts, and de Cholnoky (1939) mentions several more. Yet it is by no means established that tumors arise with greater frequency in ectopic mammary glands than in normally situated ones.

POLYTHELIA AND POLYMASTIA IN SUB-HUMAN PRIMATES

In contrast to the voluminous literature relating to supernumerary mammae in the human, there is a surprising paucity of information concerning their occurrence in many lower forms, and the writer has been able to find only eight reports of supernumerary nipples in sub-human primates.

Sutton (1889) reported two cases in monkeys (a female *Macacus sinicus* and a male *Cercopithecus patas*), both accessories being on the left side, about one inch below the normal nipple. Schickele (1899) found a case of hyperthelia (in *Macacus cynomolgus*) among twenty-eight old world monkeys and five cases among twenty-two platyrrhines of various species, all the supernumerary nipples occurring below the normal ones. Each of these animals had an extra nipple on the left side, and in three the accessories occurred bilaterally, one of them (*Cebus hypoleucus*) having two pairs. Two years later Beddard (1901) exhibited the skin of a female monkey (*Cercopithecus schmidti*) which possessed a pair of additional mammae below the normal pair, and the right supernumerary was said to be fully as large as the normal one. Zuckerman (1935) found an extra nipple (right side, below the normal gland) in a pig-tailed macaque (*Macacus nemestrinus*), and three cases of supernumeraries in baboons (*Papio porcarius*). In one animal the accessories were bilateral. An instance of hyperthelia has also been reported (Owen, 1868) in an orang-utan (*Pithecus satyrus*), the accessory nipple occurring on the left

FIG. 1. MONKEY NO. 118. TYPICAL SUPERNUMERARY NIPPLE, BELOW RIGHT NORMAL NIPPLE

side below the normal one. Coolidge (1933) found a case of bilateral supernumerary nipples, occurring below the normal ones, in a chimpanzee. This was the only case that was observed among over 600 hides of great apes that he examined. (In a report now in preparation, which the present writer has very kindly been allowed to read in preliminary draft, H. J. Coolidge, Jr. will describe an additional case of hyperthelia in a chimpanzee, as well as, for the first time, supernumerary nipples in a Siamang and a Gibbon.) Elder (1936) added an interesting case of bilateral

hyperthelia (below the normal nipples) in a female chimpanzee, which gave birth to a male offspring which showed the same distribution of accessory nipples as the mother. This case is of additional interest in that the mother was the half-sister of twins.

Only two cases have been reported of supernumerary nipples in the rhesus monkey (*Macaca mulatta*). Hartman (1927) described the first in a mature female, and Zuckerman (1935) reported a case in a young male. In both instances the extra nipple was on the left side, below the normal one.

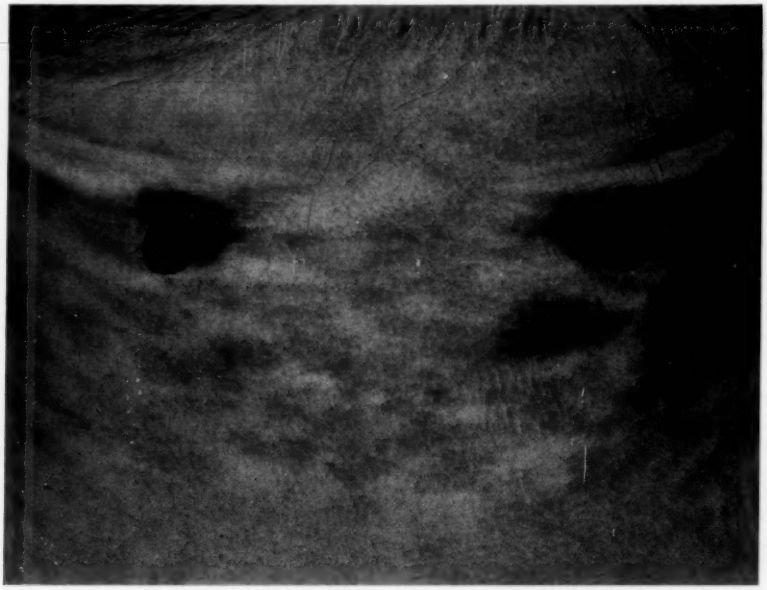


FIG. 2. MONKEY NO. 593. SUPERNUMERARY AREOLA, BELOW LEFT NORMAL NIPPLE

Personal observations

While a guest at the Embryological Laboratory of the Carnegie Institution in Baltimore, the writer was extended the opportunity of studying the huge collection of rhesus mammary glands which had been acquired by Dr. Carl Hartman over a period of years, as well as the breasts of the intact macaques which comprise the large Carnegie colony at present. Dr. Hartman has long been interested in the subject of polymastia and has, in addition, collected pertinent notes and photographs which he very kindly placed at the writer's disposal. In all, thirteen cases of supernumerary mammae have been observed, in addition to the case previously published by Dr. Hartman.

Approximately one thousand rhesus monkeys have passed under scrutiny in the Carnegie and associated laboratories. Thus, the incidence of this condition is about 1.4 per cent, or within the same range as the most reliable estimates for the human. All occurred in the thoracic region, along the approximate course of the embryonic milk line. In eleven cases the supernumerary was unilateral, and in two cases bilateral and symmetrical. Of the unilateral accessories, six occurred on the left side and five on the right. All were below the normal breast. This again agrees well with most statistics concerning the incidence of distribution in the human. Twelve of the thirteen cases were females, but this figure is of little significance, since the vast majority of the monkeys in the colony have been females.

In most instances the supernumerary nipple was distinctly smaller than the normal one. Fig. 1 shows a typical example. All gradations in size were observed, however, from a bare accessory areola (Fig. 2) to a supernumerary nipple which was indistinguishable from the normal one.

The accessory breasts were removed, either at operation or at autopsy, in one piece with the ipsilateral normal breast. The nipples were sectioned longitudinally and studied microscopically. The surface epithelium was often found to be thinner in the accessory nipples than in the normal ones. Otherwise, little histologic difference between the two was detected. The underlying fascia was dissected under the binocular microscope, to determine the presence or absence of mammary parenchyma in connection with the supernumerary nipple. In only 5 instances was there any accessory glandular tissue present, and this usually consisted of only a few short ducts radiating from the base of the nipple. There was no continuity between the normal and supernumerary mammary glands. Fig. 3 shows a mount of a typical supernumerary gland, consisting of two short ducts, and indicates its relation to the lower border of the ipsilateral normal gland.

No definite statement can be made concerning the hereditary aspects of polythelia or its possible relation to multiple births in the rhesus monkey. Two animals warrant brief mention, however, because of the strong probability that they were twins, or at least sisters. Monkeys nos. 272 and 273 arrived together in the same shipment from an animal dealer in New York City. They possessed bilateral supernumerary nipples and appeared so similar in all other respects that the animal keepers, who can ordinarily tell the monkeys in the colony apart with little difficulty, were unable to distinguish between them. Although actual proof is lacking, the presumption is strong that they had a common parentage.

In Zuckerman's report (1935) mention is made of the increase in the prominence and color of a supernumerary nipple of a male rhesus monkey following injections with estrin. This demonstrated the responsiveness of the structure to estrogenic hormone. It has recently been shown (Lamar and Speert) that the macaque nipple responds in a striking manner to the local application of an alcoholic solution of estrogen, when the nipple is painted daily with the hormone. This type of treatment was applied to the accessory nipples of 2 monkeys. Monkey L1 was an immature male with a small accessory on the right side (Fig. 4). The accessory nipple and the left normal one were painted daily with an alcoholic solution of estrone, 0.05 mg. per c.c., for 44 days. The right normal nipple was used as a control and was painted daily with plain alcohol. The results of treatment are shown in Fig. 5 and 6. There was a distinct increase in size and color of the supernumerary nipple, but the growth was somewhat less than that attained by the left normal nipple. This suggests that the supernumerary nipple, although responsive to estrogenic hormone, is either not as sensitive or lacks the same capacity for growth as the normal nipple.

Monkey no. 708 was a mature female with a large accessory nipple on the right side, of approximately the same size as the normal nipple. This

FIG. 3. MONKEY NO. 313. WHOLE MOUNT OF SUPERNUMERARY MAMMARY GLAND, CONSISTING OF ONLY TWO SHORT DUCTS; SHOWING RELATION TO LOWER BORDER OF LEFT NORMAL MAMMARY GLAND

Alum cochineal; × 3.

animal was similarly treated with local application of estrogenic hormone to the accessory nipple, but there was no demonstrable increase in size. This may possibly be explained on the basis of the nipple's having attained its maximal growth before treatment was begun. When the mammae were dissected a well-developed gland, with extensive arborization of the ducts and many end-buds, was found underlying the supernumerary nipple. This was the largest supernumerary gland in the entire series, and it extended to the lower border of the ipsilateral normal gland. It is possible that the accessory gland may have attained this size independently of the treatment. It has recently

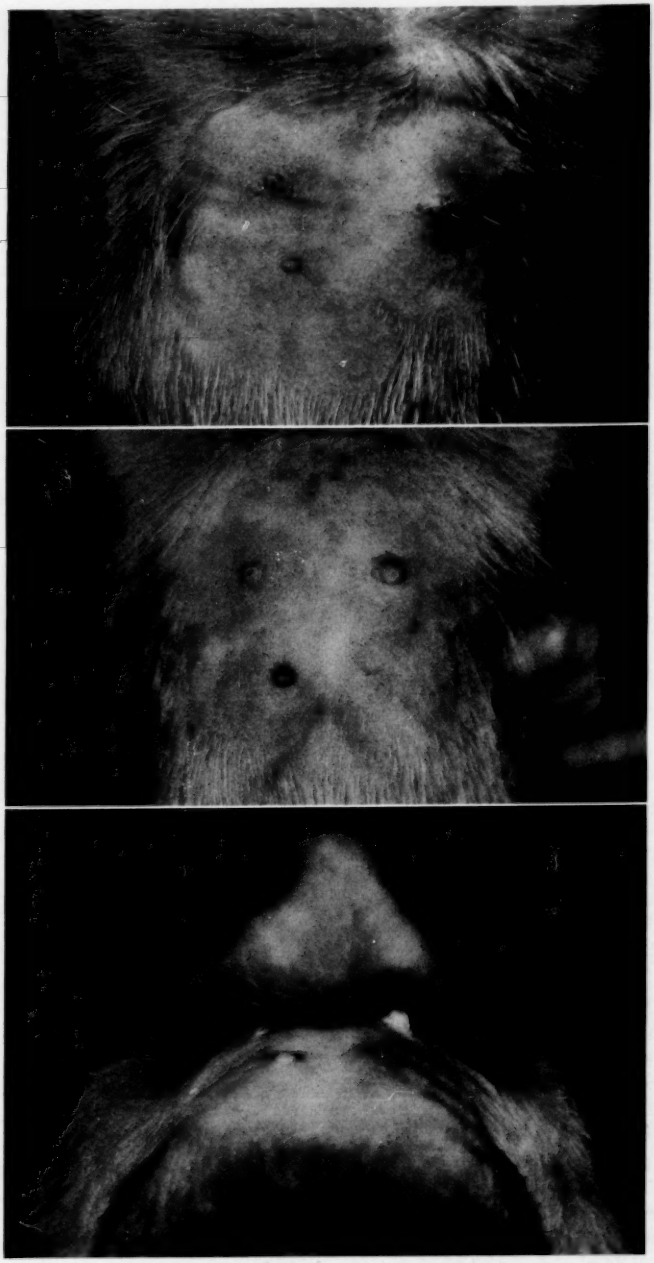


FIG. 4–6. MONKEY L1, IMMATURE MALE. EFFECTS OF DAILY APPLICATION OF ALCOHOLIC SOLUTION OF ESTRONE 0.05 mgm. per c.c., to left nipple and to right supernumerary, for forty-four days. The right normal nipple was treated with plain alcohol.

Fig. 4 (top). Before treatment. Figs. 5 (center) and 6 (bottom). After treatment.

been found, however, (Speert, 1940) that localized parenchymal growth of the monkey mammary gland may be affected by the application of estrogenic hormone to the nipple area, and it is likely that this treatment was responsible for the extensive glandular development observed.

SUMMARY

The occurrence and significance of supernumerary mammae in the human have been discussed, with special regard for the various views which have been held concerning their etiology, and for the statistical data which have been amassed relating to their incidence and location. The hereditary aspects of polymastia and polythelia are reviewed, and the theories associating these anomalies with fecundity and multiple births, tuberculosis, left-handedness, and congenital abnormalities are discussed. Some clinical aspects of this condition are also briefly mentioned.

The reported instances of accessory nipples in sub-human primates are reviewed. Only two cases have been observed previously in the rhesus monkey, and thirteen more are reported for this species. The incidence of supernumerary nipples in the rhesus monkey was found to be approximately 1.4 per cent, a figure in agreement with most recent estimates of the incidence of this condition in the human. Eleven of the thirteen animals in the present series had unilateral supernumerary nipples; in two the supernumeraries were bilateral. Supernumerary nipples were observed with about the same frequency on the two sides of the body. In only five instances was accessory glandular tissue associated with the accessory nipples.

Supernumerary nipples were found capable of responding, by growth and increased color intensity, to the local application of estrogenic hormone.

LIST OF LITERATURE

AHLFELD, F. 1880. Die Missbildungen des Menschen. *Leipzig*, s. 110.

BARDELEBEN, K. 1891. Die Häufigkeit überzähliger Brustwarzen (Hyperthelie), besonders beim Manne *Verhandl. d. anat. Gesellsch., Jena*, Bd. 5, S. 242–250.

——. 1893. Massenuntersuchungen über Hyperthelie beim Manne. *Verhandl. d. anat. Gesellsch., Jena*, Bd. 7, S. 171–185.

BEDDARD, F. E. 1901. *Proc. Zool. Soc. Lond.*, vol. 1, pp. 87–88.

BELL, A. G. 1923. Saving the six-nippled breed. *J. Hered.*, vol. 14, pp. 99–111.

BIRKENFELD, W. 1932. Beitrag zur Zwillingspathologie der Mamma. *Arch. f. klin. Chir.*, 1932. Bd. 168, S. 568–576.

BOENHEIM, F. 1919. Über das Vorkommen überzähliger Mamillen und Kombination derselben mit anderen Degenerations-Zeichen. *Anat. Hefte*, Bd. 57, Abt. 1, S. 583–609.

BONNET, R. 1892. Die Mammarorgane im Lichte der Ontogenie und Phylogenie. *Anat. Hefte*, Bd. 2, Abt. 2, S. 604–658.

BRESSLAU, E. 1909. Der Mammarapparat. *Anat. Hefte*, Bd. 19, Abt. 1, S. 275–349.

BRUCE, J. M. 1879. On supernumerary nipples and mammae; with an account of sixty-five instances observed. *J. Anat. and Physiol.*, vol. 13, pp. 425–448.

CASTLE, W. E. 1924. The genetics of multi-nippled sheep. *J. Hered.*, vol. 15, pp. 75–85.

CHAMPNEYS, F. H. 1886. On the development of mammary functions by the skin of lying-in women. *Med.-Chir. Tr., Lond.*, vol. 69, pp. 419–442.

DE CHOLNOKY, T. 1939. Supernumerary breast. *Arch. Surg.*, vol. 39, pp. 926–941.

COOLIDGE, H. J., JR. 1933. Symmetrical supernumerary mammae in a chimpanzee. *J. Mammology*, vol. 14, pp. 66–67.

DARWIN, C. 1868. The variations of animals and plants under domestication. *London*, vol. 2, p. 57.

——. 1871. The Descent of Man. *New York*, Pt. 1, p. 120.

DEAVER, J. B., and MCFARLAND, J. 1917. The Breast: Its Anomalies, Its Diseases, and Their Treatment. *Philadelphia*, pp. 51–101.

ELDER, J. H. 1936. Report of a case of inherited polymastia in chimpanzee. *Anat. Rec.*, vol. 65, pp. 83–88.

FLECHSIG, R. 1840. Ueber Polymastie oder die Vielbrüstigkeit bei Menschen. *Neue Ztschr. f. Geburtskunde*, Bd. 9, S. 12–74.

GEOFFROY SAINT-HILAIRE, M. I. 1832. Histoire générale et partic. des anomalies de l'organisation chez l'homme et les animaux. *Paris*, T. 1, p. 710.

GRAHAM-CAMPBELL, R. 1936. Polythelia. *Brit. M. J.*, Pt. 1, p. 471.

HANDYSIDE, P. D. 1873. Notice of quadruple mammae,—the lower two rudimentary,—in two adult brothers. *J. Anat. and Physiol.*, vol. 7, pp. 56–59.

HANSEMANN, D. 1889. Ueber Polymastie. *Verhandl. d. Berl. Gesellsch. f. Anthrop.*, S. 434–443.

HARTMAN, C. G. 1927. A case of supernumerary

nipple in *Macacus rhesus*, with remarks upon the biology of polymastia and polythelia. *J. Mammology*, vol. 8, pp. 96–106.

HATHAWAY, J. H. 1909. Occurrence of supernumerary nipples in the male, based on an examination of college students. *Anat. Rec.*, vol. 3, pp. 265–267.

HIRSCHLAND, L. 1898. Beiträge zur ersten Entwicklung der Mammarorgane beim Menschen. *Anat. Hefte*, Bd. 11, Abt. 1, S. 221–243.

HIRST, B. C. 1912. A Text-Book of Obstetrics. Seventh ed. *Philadelphia*, p. 706.

HOEPFNER, L. 1899. Über Vorkommen und mikroskopisches Verhalten überzähliger Brustwarzen beim Menschen, besonders beim Manne. Inaug.-Diss., *Jena*.

HUG, J. 1908. Sitz und Vorkommen überzähliger Brustdrüsen und Brustwarzen beim Weibe. Inaug.-Diss., *Strassburg*.

IWAI, T. 1906. *In* Editorial, "Polymastie et tuberculose." *Presse méd.*, T. 14, p. 650.

——. 1907a. A statistical study on the polymastia of the Japanese. *Lancet*, Pt. 2, pp. 753–759.

——. 1907b. Relation of polymastia to multiparous birth. *Lancet*, Pt. 2, pp. 818–820.

——. 1907c. Relation of polymastia to tuberculosis. *Lancet*, Pt. 2, pp. 958–960.

KAJAVA, Y., SCHRODERUS, M., WALLENIUS, M., and WICHMANN, S. E. 1921. Das Vorkommen überzähliger Milchdrüsen bei der Bevölkerung in Finland. *Acta Soc. med. fenn. duodecim.*, Bd. 2, S. 1–163.

KAYSER, F. 1908. Achselhöhlenbrüste bei Wöchnerinnen. *Arch. f. Gynak.*, Bd. 85, S. 459–482.

KLINKERFUSS, G. H. 1924. Four generations of polymastia. *J. A. M. A.*, vol. 82, pp. 1247–1248.

LAMAR, J. K. AND SPEERT, H. Unpublished.

LANDAUER, W. 1939. Supernumerary nipples, congenital hemihypertrophy and congenital hemiatrophy. *Human Biol.*, vol. 11, pp. 447–472.

LEICHTENSTERN. 1878. Uber das Vorkommen und die Bedeutung supernumerärer (accessorischer) Brüste und Brustwarzen. *Virchows Arch. f. path. Anat.*, Bd. 73, S. 222–256.

MARIE, M. P. 1893. Mamelon surnuméraire transmis héréditairement dans une famille; coïncidence avec plusiers grosses gémellaires; reversion atavique à—ou création d'un—type polymastie et polygène (?). *Bull. et mém. Soc. med. d. hop. de Par.*, T. 10, pp. 457–459.

MCGILLICUDDY, T. J. 1891. The mammae and their anomalies. *Med. Rec.*, vol. 40, pp. 446–449.

MECKEL VON HEMSBACH, H. 1852. Pathologische Anatomie der Brustdrüse. *Illust. med. Ztg.*, Bd. 1, S. 141–155.

NEUGEBAUER, F. L. 1886. Ein bisher einzig dastehende Beobachtung von Polymastie mit 10 Brustwarzen. *Centralbl. f. Gynäk.*, Bd. 10, S. 729–736.

OWEN, R. 1886. Anatomy of Vertebrates. *London*, vol. 3, p. 780.

PÉTRIGNANI, R. 1939. Polymastie et gémellité. *Bull. Soc. gynéc. et d'obst.*, T. 28, pp. 306–307.

RITZMAN, E. G. 1933. The multinipple trait in sheep and its inheritance. *New Hamp. Exp. Sta. Tech. Bull.* 53.

SATO, K. *Quoted* by Iwai, T. 1907a. *Lancet*, Pt. 2, pp. 753–759.

SCHICKELE, G. 1899. Beiträge zur Morphologie und Entwicklung der normalen und überzähligen Milchdrüsen. *Ztschr. f. Morphol. u. Anthropol.*, Bd. 1, S. 507–546.

SCHMIDT, H. 1897. Ueber normale Hyperthelie menschlicher Embryonen und über die erste Anlage der menschlichen Milchdrüsen überhaupt. *Morphol. Arb.*, Bd. 7, S. 157–199.

SCHMITT, H. 1898. Ueber die Entwicklung der Milchdrüse und die Hyperthelie menschlicher Embryonen. *Morphol. Arb.*, Bd. 8, S. 236–303.

SCHULTZE, O. 1892. Ueber die erste Anlage des Milchdrüsen-apparates. *Anat. Anz.*, Bd. 7, S. 265–270.

SEITZ, L. 1909. Ueber die sogenannte Achselhöhlenmilchdrüse und deren Genese; Schwangerschaftsmetamorphose der Schweissdrüsen. *Arch. f. Gynäk.*, Bd. 88, S. 94–131.

SPEERT, H. 1940. Mode of action of estrogens on the mammary gland. *Science*, vol. 92, pp. 461–462.

STANNUS, H. S. 1914. Congenital anomalies in a native African race. *Biometrika*, vol. 10, pp. 1–24.

STIER, E. 1912. Ueber Hemiatrophie und Hemihypertrophie nebst einigen Bemerkungen über ihre laterale Lokalisation. *Deutsche Ztschr. f. Nervenh.*, Bd. 44, S. 21–64.

SUTTON, J. B. 1889. Supernumerary mammae and nipples in man, monkeys, cows, etc. *Am. J. M. Sc.*, vol. 97, pp. 247–257.

TIFFANY, L. M. 1901. *In* Ref. Handb. Med. Sc., vol. 2, pp. 471–472.

WALTER, H. E. 1902. On transitory epithelial structures associated with the mammary apparatus in man. *Anat. Anz.*, Bd. 22, S. 97–111.

WEITZ, W. 1925. Studien an eineiigen Zwillingen. *Ztschr. f. klin. Med.*, Bd. 101, S. 115–154.

WIEDERSHEIM, R. 1908. Der Bau des Menschen als Zeugnis für seine Vergangenheit. Tübingen, S. 23–37.

WILLIAMS, W. R. 1894. Diseases of the Breast. *New York*, pp. 43–81.

WOODMAN, W. B. 1868. Three cases of a third nipple in the human subject—one case hereditary. *Tr. Obst. Soc. Lond.*, vol. 9, pp. 50–51.

ZUCKERMAN, S. 1935. Supernumerary nipples in monkeys. *J. Mammology*, vol. 16, pp. 229–230.

NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to B. H. Willier, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *Department of Biology, Homewood Campus, The Johns Hopkins University, Baltimore, Maryland, U. S. A.*

BIOGRAPHY OF A STATESMAN

Being a review of *William Henry Welch and the Heroic Age of Medicine* by Simon Flexner and James Thomas Flexner. New York (The Viking Press), 1941. 9¼ x 6⅛; x + 539. $3.75.

By *William Travis Howard, Baltimore, Maryland.*

This work, authoritative, well-arranged, and written *con amore*, is easy reading. The text is not marred by footnotes, references to the sources being given conveniently in an appendix.

Fortunate in life, Welch is also fortunate in his biographers who, fortified by a wealth of material and a long and intimate association, portray over a period of eighty-four years the progressive development of a great personality under a rapidly changing environment in science, medicine, hygiene, and social conditions. With absorbing interest they trace the evolution of the man, intellectually, spiritually, and socially, and step by step they indicate the paths which led up to the commanding rôle he played in the changes for the better, especially in medicine and hygiene, from the crude conditions of 1870 to those we now enjoy.

Of those now living who had the privilege of associating with Welch, many will find here details of his life with which they were unacquainted; others will be disappointed that some of his characteristics which they particularly valued are not more fully stressed; and still others will doubtless think that undue space is given the minutiae concerning the development of medicine and medical teaching during Welch's life time and the numerous scientific and philanthropic organizations which he served and to such a great extent guided. However, this is a matter of judgment in method and selection with which this reviewer finds himself in sympathy.

Born in 1850, in Norfolk, Connecticut, in the beautiful Litchfield Valley, Welch sprang on the paternal side from sturdy stock abundantly identified with medicine. Besides his father, two great uncles and four uncles were physicians. Welch's father, a successful physician well in advance of his time, served his community in the State Legislature and in the United States House of Representatives and was interested as well in banking and manufacture. His mother, of Huguenot extraction on her father's side, was a woman of talent and distinct literary gifts. Delicate in health, she died early, leaving a daughter of two and a half years and William Henry, aged six months.

Cared for by his grandmother, a deeply religious woman, until his fourteenth year, Welch was sent to boarding school and thence to Yale where he made his mark, graduating in 1870, second in his class.

It is a far cry from the rural Connecticut boy, indoctrinated in the then current Jonathan Edwards brand of religion, who in his college days was the author of the "Decay of Faith," to the natural scientist of maturer years, the exemplar of critical analysis of closely observed facts, tested and expanded by controlled experiment where possible and the whole submitted to the strict forms of logic, who in his old age kept Rabelais's works on his bedside table.

Disappointed on graduation in obtaining a tutorship in Greek, his favorite study, and after teaching school for two years, with great reluctance young Welch became apprenticed to his father in medical practice. In 1872 he returned to Yale for a course in laboratory chemistry, and the following fall he entered on medical studies at the College of Physicians and Surgeons in New York where he won distinction. Here he was particularly interested in normal and pathological anatomy and neurology. Even before graduating in 1875 and prior to the formal opening of the Johns Hopkins University, young Welch visited Baltimore to seek an appointment in pathology. Throughout his several years of study in chemistry anatomy, physiology, pathological anatomy, and gen-

eral pathology in Strassbourg, Leipzig, and Breslau under some of Germany's leading masters in these subjects and later during his early struggles in teaching pathology in New York, Welch ever had this goal in mind. During these student years, he found time to indulge his taste for music, painting, and architecture, and thus laid the foundation for the deep interest in general culture which later opened the door for associations and friendships of the most diverse types. With his fine and well-disciplined mind and his broad training, Welch was *facile princeps* among the younger men interested in the scientific side of medicine in America when, having attained the coveted professorship of pathology in the new University, he opened his laboratory in Baltimore and set to work to introduce to his native land the methods of teaching and investigation of the German universities.

With but little hesitation, he put behind him the lure of money-mart medical practice and social distinction in New York to undertake the inauguration of pathology as a scientific discipline in an infant university in a provincial town.

Welch was a man of general rather than special talent, who could have made his mark in any one of several fields. With a consuming curiosity for knowledge, he spread his talents over a variety of interests: science, literature, pictorial and plastic art, music, and architecture. A master of the techniques of anatomy, physiology, pathological anatomy, general pathology, bacteriology, and animal parasitology, he invented no new methods opening up avenues of discovery in any of his chosen interests.

His happiest years were probably those between 1884 and 1894 when, free from administrative duties and outside demands and surrounded by an enthusiastic band of talented associates and pupils, he was prosecuting and stimulating productive research. The senior author's description and evaluation of Welch's scientific contributions and teaching methods constitute a valuable section of the book.

The organization of the Medical School was the opening wedge between Welch and his beloved laboratory, and by the turn of the century, he had become a national figure, and his abilities and energies were swept, perhaps against his will, into a rapidly growing multitude of outside activities: medical and scientific societies, foundations for scientific investigation, and philanthropic institutions—local, national, and international. These activities involved much travel and the delivery of innumerable addresses, many of which were written overnight on trains.

Significant of Welch's dominating influence upon the Johns Hopkins Hospital in the early days is the fact that although the clinical departments were presided over by such talented and individualistic men as Halsted, Osler, and Kelly, the tone of the institution was set by the pathological laboratory. Indeed, perhaps the most striking feature of the research upon which the reputation of the Hospital was so largely based was its close coordination of the clinic with the laboratory. Halsted who worked out his aseptic technique in the laboratory and his assistant, Cushing, were experimental pathologists of note. Osler was a trained pathological anatomist, and his early residents, Lafleur and Thayer, had tables in the Pathological. From Kelly's Clinic, Whitridge Williams, Robb, Griskey, and Cullen made important contributions in the bacteriology and pathology of the female generative organs. With every phase of the work of both clinic and laboratory, Welch was in intimate touch.

Nor when the medical school opened with brilliant and productive heads of the laboratories of anatomy, physiology, and pharmacology, did the pathological laboratory under Welch suffer by comparison.

After most men retire, Welch established two new schools in the Johns Hopkins University—the School of Hygiene and Public Health and the Institute of the History of Medicine. Here he showed the same judgment and breadth of view which marked the organization of the medical school. Asking nothing for himself, he never strained his great influence to further his own University above other interests. Although meticulously careful of even the minutest details in his investigations and his editorial functions, in the administration of his laboratory and of the various schools he organized in the University and in his numerous outside activities the details were left to others.

Very popular with women and holding them in high regard, he remained celibate. Welcomed in many homes, he never had one of his own, prefering to live in "rooms" (bedroom, bath, and study), always near his clubs where he took his meals and did his frequent entertaining.

A gap in the narrative, which, to a certain degree, the present reviewer can fill, concerns Welch's associates, medical and social, during his early years in Baltimore. His association with President Gilman, while cordial, was never intimate. Indeed, Gilman had no intimates, and his position in Baltimore was one of aloofness. Having picked his men and given them opportunities, he left them free. Among the faculty of the natural sciences, with Remsen, the chemist, Rowland, the fox-hunting physicist, and Brooks, the talented but retiring zoologist, Welch's relations were friendly but not close. His cousin, Huntington Williams, who urged him to accept the Hopkins offer, died only too soon. Considering Welch's early love of Greek, it seems strange that Gildersleeve and he were not close associates. Newell Martin, head of the Department of Biology, whose laboratory gave space to Welch during his first year in Baltimore, was perhaps his only intimate on the faculty. Yet, Welch's secondary motive in accepting the Hopkins Chair was for comradeship with men of this type. However, all his colleagues with the ex-

ception of Gildersleeve were absorbed in their own pursuits with their reputations to make, and all except Martin were married. Furthermore, Welch at once fell under two influences which affected his after life in Baltimore. In the first place, he was elected to membership in the then exclusive Maryland Club the members of which represented the Maryland aristocracy in birth, breeding, and accomplishment, with a sprinkling of men of similar qualities from without the State, chiefly from Virginia and South Carolina. He was probably proposed by Doctor Alan P. Smith, grandson of the founder of the Yale Medical School, a surgeon of distinction, and the only physician appointed by Johns Hopkins on the original Board of Trustees of the Hopkins Hospital. Welch's "rooms" were near the Club and within a stone's throw of the homes of many of the leading medical men. At the Club, he associated not only with influential physicians but with several of the trustees of the University and Hospital, including Judge Dobbin, President of the Board. Here he met Major Richard Venable, eminent lawyer, cultivated Virginia gentleman, unreconstructed rebel, and boisterous wit, who with Halsted became the men dearest to his heart.

Almost immediately Welch was adopted by the medical profession of Maryland; at the first vacancy he was elected to the Medical Reunion, a supper club composed of the leading physicians, and within five years he was chosen president of the Medical and Chirurgical Faculty of Maryland, an honor reserved for the most distinguished among the membership.

From the very start of his Baltimore life, Welch was received socially and professionally with open arms and thus early was his universality recognized. Of jealousy there was none, and his popularity in ever spreading circles never waned.

Halsted, his friend of the New York days, joined him in 1886, took rooms next door, and belonged to the same circle at the Maryland Club.

In the early days of the Hopkins Hospital, the medical profession was justly antagonistic. But the authors are quite excusably in error in attributing this to the fact that three outsiders were chosen for the principal clinical posts. All the active heads of the various departments and their assistants in the dispensary, were Baltimoreans. Some like Theobald, McKenzie, Booker, James Brown, and Morison, were leaders in their specialties with national reputations. In obstetrics, gynecology, and surgery, the leading local men were too old even if asked to have undertaken the burden. In medicine, there was only one man, I. E. Atkinson, who might have reasonably aspired to a principal chair. Halsted, in surgery, was hardly an outsider. He had been working in Welch's laboratory for three years, and having no office could not be looked upon as a competitor. The antagonism had its source in two circumstances: What was considered President Gilman's over fulsome praise of Osler and Kelly, and, much more important, the dispensary was soon flooded with patients able and accustomed to pay their physicians. These grievancies were soon assuaged by the appointment of a number of the leaders in the profession as consultants to the Hospital and by better control of the dispensary clientele.

As had been the case with Welch's laboratory, the dispensary services and clinics of Halsted, Osler, and Kelly soon became the Mecca of the younger men of the profession.

Welch's career is unique in American medicine. Distinguished for his scientific contributions, his influence as a teacher and organizer of three different departments in the University, he was in the correct sense of the term a great statesman. This country has produced two other men who similarly and justly attained universal respect and beneficent influence in homage to their minds, characters, and attainments, and their unselfish devotion to the public interest in their respective fields of activity. In following Welch's career, one is tempted to think of him as a happy combination of these two philosophers—Franklin and Jefferson. Welch was of much the same body build as Franklin and was endowed with the same vigor and capacity for hard work. He possessed the same insatiable and universal mental curiosity, the love of learning, the bonhomie, the poise, the patience, and the wisdom so characteristic of Franklin. Like the latter, he attained world-wide reputation in natural science, and like him, too, even up to the end of life, he was constantly called on to advise and to guide new movements. Like Franklin, also, Welch combined geniality and hospitality with personal dignity and was above self-seeking and jealousy. The honors that came to both were unsought and were borne with becoming modesty. Like Jefferson, Welch loved all that is elegant in life and beautiful in nature and art. They shared the same aspirations for the improvement of mankind and exercised the same caution against proceeding faster in reform than conditions seemed to warrant. In Jefferson's milieu, Welch might well have written the bill of religious freedom, have planned a system of education based on the free grammar school, the county academy at which exceptionally brilliant boys would be supported at public expense, all topped by a state university, presided over by scholars, in which the students attended the "schools" of their choice in any order they chose. Similarly, Welch might well have obtained vaccine virus from Waterhouse and in the Montecello neighborhood, without medical assistance, have made observations on the evolution of the lesions of vaccinia which for preciseness are unsurpassed. As Jefferson was the political "Sage of Montecello," so Welch became the "Medical Sage of St. Paul Street," to whom came persons from near and far seeking advice in education, medicine, hygiene, and philanthropy.

By those now living, who knew and loved Welch, this account of his life will be received with gratitude. Those who knew of him only as a great man will learn wherein his greatness lay. Biologists will greet a great biologist. All readers will recognize not only an energetic, forceful character, but a wise, generous, and lovable man who more than deserved the unique national and international tributes paid him on his eightieth birthday, and will understand why Venable on his deathbed said, "I want to express my admiration for Doctor Welch," and why Halsted said on a great occasion given in his own honor, "All that I have accomplished in my scientific investigations I owe to the example and guidance of Doctor Welch," and why Councilman once said, "I would lay down my life for Welch."

BRIEF NOTICES

EVOLUTION

A Miocene Flora from Shantung Province, China. *Part I. Introduction and Systematic Considerations. Part II. Physical Conditions and Correlation. Carnegie Institution of Washington Publication No. 507. Contributions to Paleontology.*

By Hsen Hsu Hu and Ralph W. Chaney. Carnegie Institution of Washington, D. C. $3.75 (cloth); $3.25 (paper). 11½ x 8¾; vi + 147 + 57 plates; 1940.

Previous to 1938 there had been no known record of the occurrence of rock of Miocene age in China proper. The discovery of deposits near Shanwang in Shantung Province have yielded large collections of fossil plants, insects, fish, frogs, turtles, and mammals. A study of the shales and the physical conditions of the region, past and present, has produced results of great significance, not only in the Tertiary history of Asia but in the history of the development of vegetation throughout the northern hemisphere. The presence of aquatic plants and numerous fish shows that the shales were largely deposited in lakes. All evidence seems to point to the Shanwang formation as being late Miocene. "It appears to have accumulated during the time units referred to the Sarmatian in Europe, and Mascall to San Pablo in North America."

The flora as now known is made up exclusively of angiosperms. Environmental factors seem to account for the absence of coniferous genera which are regularly present in the Tertiary floras of China, Japan, and Siberia. Omitting the herbs, which form a small portion of the flora, the ratio of trees to shrubs is 45 to 55. This relationship is "extremely high for a flora containing so many temperate genera, and corresponds to that of the tropical forest near Manila. The relatively large proportion of vines is a characteristic of warm, moist habitats."

The 50 plates accompanying the systematic part of this study give a fine pictorial record of the flora from the deposits. The seven plates in the second part show topography and modern vegetation in the immediate vicinity of the fossil locality and elsewhere in North China and Japan. Both parts are well documented.

Speciation in the Avian Genus Junco. *University of California Publications in Zoölogy, Volume 44, Number 3.*

By Alden H. Miller. University of California Press, Berkeley and Los Angeles. $3.00. 10¼ x 6⅝; 262; 1941 (paper).

In this exhaustive review of the genus *Junco*, the writer has not formulated his conclusions on museum specimens alone, as is usually the case in most works of this nature, but has supplemented his data with actual field observations. The yellow-eyed juncos consist of the *alticola* and *phaeonotus* groups (*artenkreis*), and the dark-eyed birds fall into the *oreganus* and *hyemalis* groups with the *caniceps* (*rassenkreis*) intermediate between the former two. In all groups there is a good correlation between wing and tail length; no other correlations of large magnitude run through all forms of juncos with constancy. No environmental correlation of color (Gloger's Law), of size (Bergmann's Law), or of size of extremities (Allen's Law) could be found.

As to the phylogeny of the genus, it appears that it arose in North and Middle America and now shows no resemblance to the Emberizinae of Europe and South America. *Vulcani* is considered a primitive stage followed by the yellow-eyed juncos. *Caniceps*-like and *hyemalis*-like forms may have arisen at the same time in the interior and in the East.

Each taxonomic form is carefully described, the range outlined, intraracial and interracial variations, and relationships discussed. The first appendix is a comprehensive review of the nomenclature, and the second lists the breeding localities of typical populations. Altogether this forms a notable contribution for a better understanding of a difficult group of birds.

Prehistoric Communities of the British Isles.

By V. Gordon Childe. W. and R. Chambers, London and Edinburgh. 20s. net. 9 x 6¼; xiv + 274 + 16 plates. 1940.

Although paleolithic sub-men have occupied the British Isles for approximately half a million years, it was only about fifty thousand years ago that men who can be definitely identified as *Homo sapiens* ap-

peared. The cultural remains of these earlier inhabitants is not adequate for the recognition of the graded stages of development such as occur in France. The earliest culture that can be correlated with a corresponding one from the continent is the Aurignacean, but this was not developed spontaneously but was introduced from the mainland.

All subsequent cultures are amply represented in Britain by such structures as barrows, cairns, brochs, etc., which are more numerous than commonly supposed. Excavation of these has yielded a great quantity of stone and clay shards, knives and spear points, urns and beakers, and from later times bobbins, bits, dice, and coins.

In the present work all of these artifacts are discussed in detail, as well as those of the pre-Aurignacean cultures. Numerous text figures and diagrammatic maps elucidate the text, and a series of excellent plates from photographs by the author add to the value of the book. Even the pre-Romanic languages come in for a share of the discussion. Of these there appear to have been seven, six of which have Keltic affinities while the relationships of the seventh, which is probably the oldest, are unknown.

The book is complete and scholarly, with extensive index and bibliography.

MAMMALS OF THE LAVA FIELDS AND ADJOINING AREAS IN VALENCIA COUNTY, NEW MEXICO. *Miscellaneous Publications, Museum of Zoology, University of Michigan, No. 51.*

By Emmet T. Hooper. University of Michigan Press, Ann Arbor. 50 cents. 10 x 6½; 47 + 3 plates; 1941 (paper).

A report of a study of the mammal fauna of a section of west-central New Mexico on and around extensive fields of blackish lava to determine the forces directing the evolution of dark races of mammals on the lava flows. In the Tularosa Basin, where the lava beds are much more isolated than those in Valencia County, the blackish pelage coloration has become more completely fixed. The study, based on records of 60 kinds of mammals (species and subspecies) indicates "(1) that the darker coloration has a higher survival value on the black lava; and (2) that the present center of dispersal of the darker animals is the black lava and not the lighter substrata near the black lava."

DEVELOPMENT OF OCCLUSION. *University of Pennsylvania Bicentennial Conference, M-12.*

By William K. Gregory, B. Holly Broadbent, and Milo Hellman. University of Pennsylvania Press, Philadelphia. $1.50. 9 x 6; 72; 1941 (paper).

GENETICS

GENETICS AND THE ORIGIN OF SPECIES. *Second Edition, Revised.*

By Theodosius Dobzhansky. Columbia University Press, New York. $4.25. 9 x 6; xviii + 446; 1941.

The first edition of this outstanding book has already been reviewed in this journal (Vol. 13, p. 211). The second edition does not need a detailed review, for the author's point of view and his arrangement of the material has remained essentially the same. Nevertheless a considerable number of additions and some changes have been made, and these deserve notice.

While most of the minor changes are the result of the author's desire to make the text more explicit, the most important changes are additions of new material. This is exemplified by the increase in the number of references from about 600 to nearly 1,000 and of the number of pages from 364 to 446. The inclusion of so much new material is the result on the one hand of the recent growth of research on evolutionary problems and on the other of the expansion of the author's interests. The inclusion in the revised edition of work on the transformations of pneumococci is a good example of this. Some changes in the arrangement of the material have been made of which the most noticeable is a shift of the material on the theoretical significance of population dynamics from the chapter on selection to a new chapter entitled "Patterns of Evolution."

Among the recent works on evolution discussed and criticized by Dobzhansky, Goldschmidt's *The Material Basis of Evolution* takes a prominent place. This is not surprising since the two authors differ even in some of their basic assumptions.

A revision at the present time of Dobzhansky's excellent book would have been welcomed in any case by biologists interested in evolution. Perhaps some of them will find it particularly valuable because it follows so closely the expression of very different views by Goldschmidt.

GENERAL BIOLOGY

BIOLOGY AND HUMAN AFFAIRS.

By John W. Ritchie. World Book Company, Yonkers-on-Hudson, New York. $2.32. 8¾ x 5½; xiv + 1026; 1941.

The encyclopedic proportions of this high school textbook (1026 pages) may at first glance frighten away some of those for whom it is intended. However, although much more material has been included than an average class can hope to cover in one year, the 22 units are, in the main, independent of each other so that they can be taken up in practically any order, or some can be omitted. The point of view is practical

throughout, the wide application of biological ideas to human living being constantly emphasized.

The teaching method combines the type, group, and principles methods. The number of scientific terms has been kept at a minimum. The author is to be especially commended for the excellent and profuse illustrations which are a distinct feature of the book. Each unit is concluded with a comprehension test, a list of suggested activities and applications, and selected references for reading. The appendix contains a classification of animal and plant kingdoms, a table of the divisions of geological time, a complete glossary, and an index.

EXPLORATIONS AND FIELD-WORK OF THE SMITHSONIAN INSTITUTION IN 1940. *Smithsonian Institution Publication 3631.*

Smithsonian Institution, Washington, D. C. Free. 9¼ x 6; 100; 1941 (paper).

Each year expeditions go out from the Smithsonian Institution to collect specimens, record data, etc. in the various fields of science. A preliminary announcement of the year's work is issued in pamphlet form. The present report shows that, as usual, much work was done in the biological sciences in 1940. Early man was traced in Virginia and Folsom man in the West, while various Indian groups in North America were studied. Live animals were collected in Liberia while extinct animals were trailed in the central Utah and the Bridges Basin of Wyoming. Grasses were studied in Venezuela, butterflies in Virginia, birds and mammals collected in South Carolina, and reptiles and amphibians in Mexico. Habitat group material was collected in the Canadian Rockies, dredge hauls made in the Gulf of California and the King crab (what we know in canned form as Japanese crab meat) studied in Alaskan waters. The many photographs form an interesting part of this brief report.

AN INTRODUCTION TO BIOLOGY.

By J. C. Cross. The C. V. Mosby Company, St. Louis. $1.90. 7½ x 5⅜; xviii + 507; 1941.

This book has been written for the special purpose of presenting southern plants and animals to students and teachers of high schools in that part of the country. Since southern fauna are rich enough to supply good examples for nearly all practical purposes, either for laboratory or for recitation, the author selected those representative forms of the biological resources of the South that would be of most value in a high school course. The textual material is divided into eight parts or units. In general, the book follows the plan of proceeding from the simpler plants and animals to the more complex. The divisions of the material are as follows: Introduction; The simplest animals; Plants without seeds; The seed-bearing plants; Animals with jointed feet; Animals with backbones; Structure and function in plants; and Structure and function in animals. There is no bibliography but an excellent glossary and index are available.

OCEANOGRAPHY OF THE NORTH PACIFIC OCEAN, BERING SEA AND BERING STRAIT: *A Contribution toward a Bibliography.*

By Mary C. Grier. University of Washington, Seattle. $2.50. 19 x 7; xxii + 290; 1941 (paper).

More than 2,930 items are listed in this bibliography. Important books, magazine articles and documents bearing upon the oceanography of the area defined and the inshore waters, with the exception of the coast of California, are given. The bibliography is divided into the following sections: General references, Physical oceanography, General biology, Plankton, Invertebrata, Pisces, Aves, Mammalia, and Flora. There are indexes to author and personal names and to subjects and titles. The volume is well printed. The generous spacing of the items not only makes for easy reading but gives opportunity to the student to jot down additional notes.

PAPERS OF THE MICHIGAN ACADEMY OF SCIENCE, ARTS AND LETTERS. *Volume XXVI (1940). Part I: Botany and Forestry. Part II: Zoology. Part III: Geography and Geology.*

Edited by Eugene S. McCartney and Mischa Titiev. The University of Michigan Press, Ann Arbor; Oxford University Press, London. Part I, $1.75; Part II, $1.75; Part III, $1.50. 9¼ x 6; Part I, vii + 158 + 3 plates; Part II, viii + 180 + 1 plate; Part III, vii + 104 + 1 plate; 1941 (paper).

Volume 26 of this series is available in four parts; the first dealing with botany and forestry, the second with zoology, and the third with geography and geology. The fourth part is concerned with topics in other than biological fields. The contributions are too numerous to mention even by subject matter. They pertain mostly to the biology of Michigan.

CINE-BIOLOGY.

By J. V. Durden, Mary Field and F. Percy Smith. Penguin Books, Harmondsworth, Middlesex, England; Penguin Books, Inc., New York. 25 cents. 7 x 4¼; 128; 1941 (paper).

"... an attempt to blend together into one narrative three sharply contrasting points of view; these are the

critical accuracy of the scientist, the exuberant enthusiasm of the naturalist, and the anthropomorphic ideas of the layman who strives to translate the doings of an insect in terms of human endeavour." For this purpose the common invertebrates have been chosen.

The illustrations are from photographs (hence Cinebiology?). The result is pleasing and readable and should be enjoyed by the layman for whom it is intended.

COLLECTED REPRINTS: 1940. *Woods Hole Oceanographic Institution: Containing also the Annual Report of the Director of 1939.*

By Various Authors. Woods Hole Oceanographic Institution, Woods Hole, Massachusetts. $3.00. 9⅞ x 7; 1941 (paper).

This volume contains those contributions from the Woods Hole Oceanographic Institution for 1940 that did not appear in *Papers in Physical Oceanography and Meteorology*. The 33 papers are unrelated to each other. Mostly they deal with the physics and chemistry of sea water, although ecology, taxonomy, and experimentation are not neglected. There is one paper dealing with the flight of birds. The annual report of the Institution is appended.

PROCEEDINGS OF THE SIXTH PACIFIC CONGRESS OF THE PACIFIC SCIENCE ASSOCIATION *Held at the University of California, Berkeley, Stanford University, and San Francisco, July 24th to August 12th, 1939. Volume III.*

Pacific Science Association. University of California Press, Berkeley and Los Angeles. $3.50. 9¼ x 6; viii + 754; 1940 (paper).

This large volume consists of many contributions on all phases of marine study. Currents, oceanography, distribution of fish, research programs, climatology, are but some of the topics. These studies have all been made on the Pacific Ocean, from east to west.

EL MAR *Acuario del Mundo.*

By Enrique Rioja. Editorial Seneca, Mexico City. $2.50. 7½ x 5½; 405; 1941.

In this book the author, a well-known Spanish student of animal life of the sea and now pursuing his research in the Biological Institute of the National University of Mexico, writes in a popular style of some of the lower plant and animal forms, coral, mother-of-pearl, fish with protective coloration or chameleon-like characteristics, and monsters, real and imaginary, of the sea. The book is written with authority as well as charm and is profusely illustrated.

MANUAL OF BIOLOGY. *Sixth Edition.*

By George Alfred Baitsell. The Macmillan Company, New York. $2.75. 8¾ x 5¾; ix + 449; 1941.

This standard biology text has enjoyed wide popularity and use through five previous editions. The present edition maintains the same high quality of workmanship exhibited by the earlier editions, and with few minor exceptions presents the same well-selected material in the same logical sequence as it appeared previously.

UNIVERITY OF COLORADO STUDIES. *Series D. Physical and Biological Sciences, Vol. I, No. 3.* Containing the Following Articles: *Keys for the Identification of Colorado Orthoptera*, by Gordon Alexander; *Effect of X-radiation upon the Growth of Lemna minor*, by Edna Louise Johnson; *Abbreviation of Names of Biological Publications*, by Edward D. Crabb; *Distribution Problems in Some Moraine Ponds*, by Hugo G. Rodeck; *An Introduction to the Limnology of Northern Colorado*, by Robert W. Pennak; *An Anomalous Everted Piece of Ileum in an Adult Cottontail Rabbit*, by Edward D. Crabb and Margaret A. Kelsall; *A Bibliography of High Altitude Limnological Investigations in the Western United States*, by Robert W. Pennak.

University of Colorado, Boulder, Colorado. $1.00. 10 x 6¾; 229; 1941 (paper).

HUMAN BIOLOGY

THROUGH CHINA'S WALL.

By Graham Peck. Houghton Mifflin Company, Boston. $3.50. 9⅜ x 5⅞; 371; 1940.

The author visited China for the express purpose of making portraits of the natives and sketching their countryside. The numerous drawings in the book were not put there to illustrate the text; rather the text was written as a commentary on the illustrations.

Peck explains that the disdain which the Chinese feel toward the Mongolian barbarians that are penetrating the frontier is equalled only by that which the barbarians feel for the Chinese. The author is equally interested in both, especially in their personal sanitation, or lack of it, a subject of which he never tires. This interest is always in the individual, never in the group. The individuals also took a great deal of interest in him, and used to assemble outside his window to make peepholes in the paper window pane, that they might witness his ablutions and admire the hair on his body, which they mistook for feathers (the Mongolians have no hair except on the head).

The last few chapters are taken up with the author's experience as a stretcher bearer and ambulance driver for the Red Cross after the actual outbreak of hos-

tilities. The account of the rescue of a fifteen-year-old boy who had been lying in the mud for a month, unprotected from the weather, with a shattered arm hanging limply from the shoulder blade, and a fly-blown and maggot-ridden leg and whose only sustenance had been what he could beg from the peasants who continued to cultivate their rice patches amid the filth and stench of the bodies of horses and human beings rotting together, should be effective in teaching the reader what war means.

But somehow one reads between the lines that even this war will pass. There have been wars in China before, but Chinese civilization has endured for three millenia and after each war it has rolled back again like the rock of Sisyphus. The war may realign all the ephemeral boundaries of Europe, it may destroy democracy and religion in the occident, it may be the tocsin of western civilization, but when it is over the author expects to see the old order in China restored, and when that occurs he is going back again.

River of Ruins.

By Louis J. Halle, Jr. Henry Holt and Company, New York. $3.00. 8½ x 5⅝; xii + 334 + 16 plates; 1941.

The unofficial expedition made by the author and a companion to the lesser explored sites of Mayan civilization in Petén, a jungle district lying partly in Mexico and partly in Guatamala, is the subject of this fascinating book. The journey was made mostly by the water routes of the rivers de la Pasión and Usumacinta. At Paso Subín the two explorers felt that they had left the outposts of present civilization. At La Libertad they divided their time between studying the ruins at two sites and an embarrassing attempt to collect bird specimens for the Harvard Museum—their only ornithological venture of the trip. At Tikal and Palenque, the eastern and western extremities, approximately, of the region explored, they found "architectural capitals" from two periods of Mayan civilization. Tikal is considered to have been the first of the cities constructed by the mature Mayan civilization; Palenque the last. Of the well-preserved sculptures on the lintels of the bat-infested temple at Yaxchilán the author writes:

I suppose these stones were designed chiefly to inspire awe, because even across all the barriers to understanding that separate us from them, they have that effect. . . . This is High Mass in any language and in any time, whatever gods it may represent. . . . All this elaboration of costume, all this wealth of artistry, the subtlety of the modeling and the devoted rendering of every detail, were designed to lift men above their common selves to the level of their common aspirations. There is more here than can be measured by any arithmetic—more than what is included in any archaeological report.

In addition to the descriptions of the ruins the book is colored by vivid descriptions of the geography, the natives and "foreigners," the vegetation, animal and insect life of the region, and numerous accounts of the explorers' adventures and misadventures.

Twentieth Century Indians.

Photographs and Text by Frances Cooke Macgregor with a Foreword by Clark Wissler. G. P. Putnam's Sons, New York. $3.00. 11 x 8⅜; xv + 127; 1941.

The stated purpose of this beautifully illustrated volume is to dispel the many vagaries and misconceptions concerning the Indians of the United States. The past century has witnessed the futile attempt on the part of the government and of the people of the United States to destroy the American Indians' native cultural, social, economic, and religious structures, and replace them with so-called "civilized" philosophies, concepts and activities. The fact that the aboriginal populations failed to successfully attain the desired measure of "civilization," and that their stocks were being rapidly depleted, seemed ample reason to believe that the Indians represented an inferior race, and that there was not much hope for them in the present world of competition.

A more recent and hopeful attitude toward the Indian accepts his culture and industry as valuable in themselves without regard to civilized culture and industry. This attitude has resulted in better methods of education and in better health and living conditions for the Indians, and these in turn are preparing them for happier and more successful lives, not as white men, but as Indians.

The author's photographic artistry has contributed greatly to the excellence of the volume. Two maps, one at the beginning and one at the end of the book, are of much interest. The first gives the habitats of the important Indian tribes at the time Columbus discovered America. The total number of Indians at that time has been estimated to be about 846,000. The second map gives the distribution of the principal Indian tribes in the United States today and marks the locations of small communities (Rancherias) in California and (Colonies) in Nevada.

Crime and Its Treatment. *Social and Legal Aspects of Criminology.*

By Arthur E. Wood and John B. Waite. American Book Company, New York. $3.50. 8¾ x 5¾; ix + 742; 1941.

As the sub-title indicates this heavy tome deals with two aspects of criminology, the sociological and the

legal. The latter is discussed in the second half of the volume wherein an informative and comprehensive account is given of the elements of criminal law and of penology—liability, evidence, trial procedures, prison systems, and corrective treatments. Thus, the complete picture is made available of the reactions of our society to the trespassing against its regulations. The supposed cause of this trespassing, i.e. crime, constitutes the substance of the first part of the book. Woods, who is responsible for this part, examines first crime statistics and their value and the case history method of study of crime. He emphasizes the unreliability of crime statistics, and in general has a low opinion of statistical handling of criminological data. So far as the etiology of crime is concerned, the author is mainly interested in the effects of the environment, although a short chapter covers briefly certain aspects of the psychopathology of crime. If this chapter had not been included one could well assume that views on criminality have not made much progress during the last century. Sociologists often accuse the human biologist of lack of appreciation of the so-called social sciences yet the ineffectiveness exhibited by the narrow viewpoint which emanates from the dominating sociological approach should encourage further experimentations along other lines. After all, crime is a behavior problem and man's behavior is rooted in his "lowly nature" as Darwin put it. A selected bibliography follows each chapter and many references are given in the text.

CULTURE ELEMENT DISTRIBUTIONS: XIII. NEVADA SHOSHONE. *Anthropological Records, Volume 4, Number 2.*

By Julian Steward. University of California Press, Berkeley. $1.50. 11 x 8½; v + 151; 1941 (paper).

CULTURE ELEMENT DISTRIBUTIONS: XIV. NORTHERN PAIUTE. *Anthropological Records, Volume 4, Number 3.*

By Omer C. Stewart. University of California Press, Berkeley. 75 cents. 11 x 8½; iii + 85; 1941 (paper).

These studies give extensive data, arranged in notes and in tabular form, on the distribution of cultural elements in Nevada Shoshone and the neighboring Northern Paiute. The habitat of the Northern Paiute is uniformly desert, although modified somewhat by streams from the mountain area. The Shoshoneans, dwelling in the region east of the Northern Paiute, occupy an extremely infertile area, which necessarily has had an important effect upon many of their activities. Their food is largely rodents and seeds, which grow widely scattered.

In summarizing and synthesizing the Shoshonean data, uniformity is shown to be greatest in the essential economic traits, such as hunting and seed-gathering: greatest variation in hunting, as in food-gathering, is in details which are dispensable to the main activity. Shamanism also has general stability. "Its secondary features such as the particular spirits and powers, ritual equipment and behavior patterns, are more variable."

Both of these studies represent careful detailed work and form valuable additions to cultural investigations on Indian tribes in or near the Great Basin.

SCIENTIFIC ASPECTS OF THE RACE PROBLEM.

By H. S. Jennings, Charles A. Berger, Dom Thomas Verner Moore, Aleš Hrdlička, Robert H. Lowie, and Otto Klineberg. With a Preface by His Excellency Bishop Joseph W. Corrigan. The Catholic University of America Press, Washington, D. C. Longmans, Green and Co., London, New York, and Toronto. $3.00. 8½ x 5¾; ix + 302; 1941.

To date it has been unavailing for students of anthropology, sociology, etc. to point out the fallacies of the pronouncements on race superiority or inferiority. The general public is willing to concede that the *others* are not superior to *us*, but no one will accept the verdict that *we* are not superior to the *others*. The latest attempt to present an objective discussion of the race question is constituted by this book. Although it is interesting and contains the writings of eminent men, its effectiveness to influence public opinion must be doubted. One reason is that, with but two exceptions, none of the authors actually deals directly with the main theme. Jennings provides an excellent summary of genetics, Berger discusses briefly the inheritance of psychological traits, Moore presents a learned survey of animal psychology investigations, Hrdlička outlines a classification of races, but only Lowie and Klineberg occupy themselves with the variation of certain traits among racial or national groups. Lowie examines and compares the cultural achievements and moral conduct of certain primitive groups, while Klineberg considers critically the results of intelligence tests made on several national groups. All the articles are praiseworthy but the last two are the only ones which seem pertinent to the theme of the symposium.

THE COLOUR BAR IN EAST AFRICA.

By Norman Leys. The Hogarth Press, London. 7s. 6d. 8½ x 5¼; 160; 1941.

That the Nazis are not the only offenders in the application of the philosophy of racial superiority in favor of their own people is well brought out in this book. It traces the history of the settlement of British East Africa, especially the two Rhodesias and Kenya, and the development of laws regulating property ownership, labor, taxation, and education. In the author's

opinion the domination of the British minority is founded on the laws and regulations which tend to discriminate against the African. These regulations limit the independent economic opportunities of the natives and at the same time give educational, social, and political privileges to the white minority.

This disparity [in educational opportunities] is defended on the ground of prestige, because at all cost the rise of a class of "poor whites" must be prevented. That means that a secure position in the ruling caste must be found for the stupidest man of European descent, but no place above the servile for the most gifted African.

Ley reinforces his arguments by a generous use of references and citations on the effects of the "colour bar" in the conduct of agricultural and mining industries and on the daily lives of the people. This is a thought-provoking treatise, whether or not the reader will agree with the author's viewpoint and suggestions for a solution of the problem.

ESKIMOLAND SPEAKS.

By William B. Van Valin. The Caxton Printers, Caldwell, Idaho. $3.50. 9 x 5⅞; 242; 1941.

In his seven years of missionary and educational work in Alaska, the author of this fascinating volume absorbed much of the psychology, industry, and humanity of the Eskimos. Of no less interest to him was the beauty of the barren arctic wastes, the colorful panorama of the midnight sun, and the magnificent eeriness of the aurora borealis.

As with all other white visitors, explorers, or missionaries in the arctic, the writer is left amazed as well as awe inspired at the success with which life in the arctic (both human and infra-human) wrings from the brutal grasp of eternal winter the necessities for its sustenance. The Eskimos' ability to survive in such an adverse environment combines the keenness of the modern scientist, the foresight of the successful economist, and the stamina of the well-trained athlete.

For those interested in polar life, this book will prove as thrilling as it is informative.

THE SOCIAL RELATIONS OF SCIENCE.

By J. G. Crowther. The Macmillan Company, New York. $3.50. 8⅜ x 5⅜; xiii + 665; 1941.

This book is an ambitious undertaking in which the author attempts to survey the scientific activities of man in prehistoric, classical, medieval, and modern times, in order to discover what social conditions are essential for the birth and growth of science. Science is regarded as a social product and the present-day need for an effective social policy for science is stressed. The material of the first two thirds of the book is essentially a descriptive historical formulation along conventional lines, with emphasis on the interdependence of social and scientific development. The last third of the book is devoted to a description of the distribution of present-day research facilities and a discussion of the social responsibilities of scientists. The style is somewhat didactic throughout. References are given at the end of each chapter and there is an index.

EAST AFRICA.

By Elspeth Huxley. William Collins, London. 3s. 6d. 8¾ x 6¼; 48; 1941.

This little volume by one who has had a long first-hand knowledge of East Africa makes interesting reading. It belongs in The British Commonwealth Series, a group of books designed to contribute to a better understanding of Great Britian and the British Commonwealth. The 12 colored plates of scenic views and 17 black and white illustrations of native life are well done, considering the low cost of the book. In the text Mrs. Huxley gives a clear picture of the many contrasting races to be found in this great region under British rule, where there are such wide divergences in religion, custom, and tradition, outlines the problems which the British Government has had to face in governing these people, and the manner in which these problems are being solved. Those familiar with the author's *White Man's Country* will regret that the volume is so brief.

THE STUDY OF MAN. *University of Pennsylvania Bicentennial Conference, M-B.*

By Lawrence J. Henderson. University of Pennsylvania Press, Philadelphia. 25 cents. 9 x 6; 22; 1941 (paper).

ZOÖLOGY

BIBLIOGRAPHIA PRIMATOLOGICA; *A Classified Bibliography of Primates Other Than Man. Part I. Anatomy, Embryology and Quantitative Morphology; Physiology, Pharmacology and Psychobiology; Primate Phylogeny and Miscellanea.*

By Theodore C. Ruch. With an Introduction by John F. Fulton. Charles C Thomas, Springfield, Illinois. $8.50. 10⅜ x 7⅝; xxvii + 241; 1941.

Serious scientific study of man's nearest animal relations, the lemurs, monkeys, and apes, has for a long time been sadly neglected. In the last few decades, however, rapid progress has been made, resulting in

the young and promising science of primatology. The accumulated knowledge in this important speciality is represented by the 4630 titles of morphological and physiological papers which have been painstakingly collected and classified in the present volume. A future, second part of this monographic bibliography will deal with pathological and taxonomic studies on primates.

In many branches of modern biology and medicine our simian cousins are rapidly replacing laboratory rodents and carnivores as experimental animals, a fact that is directly responsible for a large share in the tremendous recent increase in primatological literature.

This scholarly bibliography is indispensable to all newcomers in primatology and will be particularly helpful in preventing repetition of work that has already been accomplished. The author has faithfully indicated under each title precisely which species of primates has been dealt with. This alone should tend to eradicate that still prevalent and harmful habit, chiefly of medical writers, in stating: "in *the monkey* I found such and such a condition." With some 600 different species of recent primates and with at times far greater differences between some monkeys and others than between some and man, it is utterly useless to record any observation on "a monkey" without giving species, sex, and age.

The carefully considered and detailed subdivisions of this bibliography are grouped under the major headings of anatomy, embryology, quantitative morphology, physiology, pharmacology, psychobiology, phylogeny, and "miscellaneous". Biology and medicine have been rendered a great service with this unique, practical, and excellently printed volume which forms a very essential part of a safe foundation on which to build in the future.

A Field Guide to Western Birds.

By Roger T. Peterson. Houghton Mifflin Company, Boston. $2.75. 7¼ x 4½; xviii + 240; 1941.

Most bird students already know Peterson's *Field Guide to the Birds*. The present volume is its counterpart for the western birds. Like its predecessor the object of the book is to enable the student to make field identifications of the birds by characteristic color patterns known as "field marks". To this end, the field marks are given emphasis in the illustrations. One must possess some knowledge as to the families of birds, but after this has been mastered, the descriptions point out the essential features for the identification of the species.

Practically all species considered are illustrated, in part or in whole, either in black or white, or in color whenever the latter is more important than pattern for identification. The descriptions are further enhanced by the inclusion of ranges of the species and the song of the bird whenever this feature is helpful, as in some of the flycatchers. It is to be regretted that the plates in many cases are not to be found close to the textual material. For instance, the plate of flycatchers is among the woodpecker descriptions and vice versa. Western fauna is very diversified and the number of geographic races is greater than in the East. The writer was hard put to meet this obstacle, but finally decided to list these forms in an appendix. In the few cases that the races can be separated in the field, the distinguishing characters are given in the text.

There is no doubt that this handy pocket (overcoat size) guide will find as enthusiastic welcome in the West as the former book did in the East. Both together will identify birds anywhere in the United States.

Animal Biology. *Third Edition.*

By Michael F. Guyer. Harper and Brothers, New York and London. $3.75. 9⅛ x 6; xix + 723; 1941.

This text has been one of the leaders in its field for a decade. The new edition (cf. Q. R. B., Vol. 7, p. 361 and Vol. 12, p. 472 for mention of earlier editions) involves a number of changes designed to increase its usefulness. Numerous sections of the book have been rewritten, some condensed, and others expanded. New material presented includes a very important chapter on ecology, which provides the student with a concise review of the field, an account of the life and structure of planarians, a discussion of ameboid locomotion, and reviews of recent experimental work, especially that on "mating types" in *Paramecium*. In addition, the section on birds has been rewritten, and the classification of mammals reorganized. A number of new illustrations have been added. The author presents the principles of biology in such a way as to retain the value of the usual "types" course, but the emphasis is upon fundamental concepts underlying all life phenomena. The well-chosen, clearly-labelled illustrations are a feature of the book. The volume is concluded with a list of reference books, a glossary, and a complete index.

Return to the River: *A Story of the Chinook Run.*

By Roderick L. Haig-Brown. Illustrations by Charles DeFeo. William Morrow and Company, New York. $3.00. Limited edition, autographed by author and illustrator, $10.00. 8⅜ x 5½; 248; 1941.

This is the fascinating story of Spring, a Chinook salmon. It tells of her birth, her travels from the

Grand Coulee region to Puget Sound and the Pacific waters beyond, and her return at the age of five years to spawn and die in the same stream where she was born. Haig-Brown, a British-Canadian ichthyologist and author of the sourcebook *The Western Angler* tells the story of the life-cycle of the salmon in the vein of a novel, but without deviating from facts. The reflections of the old Senator, who was a witness of Spring's birth and death, offer sidelights on the salmon industry and on the use and misuse of natural resources, and conjectures on the possible effects of the completion of the Columbia River dam projects on the survival of the salmon in the Northwest. The illustrations by Charles DeFeo are unusually fine and a fitting accompaniment to the narrative.

WATCHING BIRDS.

By James Fisher. Penguin Books, Harmondsworth, Middlesex, England; Penguin Books, Inc., New York. 25 cents. 7⅛ x 4¼; 192; 1940 (paper).

A bird's eye view of the field of ornithology, its problems, and its methods of study are contained in this little book. After introductory chapters to the class Aves, there follow chapters on migration, on the numbers of birds, their habitats, their territory and breeding cycles, and their behavior. Although it would be impossible to treat all these subjects thoroughly in such a small amount of space, the review has been ably presented for the beginner. Since the writer is British most of the examples are taken from British birds, but the principles are the same for birds of any area.

INSECTS AND THEIR STORIES.

By Harry Hoogstraal. With Camera Studies by Melvin Martinson and Drawings by Carl O. Mohr. Thomas Y. Crowell Company, New York. $2.00. 7½ x 9¼; 144; 1941.

In this fascinating little volume are recorded, in language understandable to the high school freshman, the stories of some 50 of our common house, garden, and forest insects. The stories include observations on the everyday activities, the favorite haunts, the methods of resisting natural forces, and the methods of replenishing the races of both land and acquatic forms.

The excellent photographic work of Martinson adds considerably to the interest and value of the book for budding naturalists. The volume is well indexed. An additional index and guide to the recognition of insects, arranged according to orders, is provided.

BUTTERFLIES. *A Handbook of the Butterflies of the United States, Complete for the Region North of the Potomac and Ohio Rivers and East of the Dakotas.*

By Ralph W. Macy and Harold H. Shepard. The University of Minnesota Press, Minneapolis. $3.00. 9 x 6; vii + 247; 1941.

The fact that no key to the Lepidoptera of the northeastern United States has appeared since 1889 is ample reason for the preparation of this excellent work. In addition to the key to 162 species of Lepidoptera, the present treatise includes many interesting details relating to the natural history, distribution, and economic importance of many of our northeastern forms. The volume is beautifully illustrated with both monochrome and dichrome photographs. The description of each species begins with a list of publications relating particularly to that species. A complete index is appended.

STUDIES ON GREGARINA BLATTARUM WITH PARTICULAR REFERENCE TO THE CHROMOSOME CYCLE. *Illinois Biological Monographs, Volume XVIII, Number 2.*

By Victor Sprague. The University of Illinois Press, Urbana, Illinois. $1.00. 10½ x 7; 144 + 6 plates; 1941 (paper).

The present investigation deals principally with the period that involves syngamy and the meiotic phenomena of this most common and widely known of the Sporozoa. It also includes an account of the process of encystment and the development of the cyst. Five excellent plates and several figures elucidate the text.

STUDIES OF THE NEOTROPICAL COLUBRINAE. *VIII. A Revision of the Genus Dryadophis Stuart, 1939. Miscellaneous Publications, Museum of Zoology, University of Michigan, No. 49.*

By L. C. Stuart. University of Michigan Press, Ann Arbor. $1.15. 10 x 6½; 106 + 4 plates; 1941 (paper).

A CONTRIBUTION TO THE KNOWLEDGE OF VARIATION IN OPHEODRYS VERNALIS (HARLAN), *with the Description of a New Subspecies. Miscellaneous Publications, Museum of Zoology, University of Michigan, No. 50.*

By Arnold B. Grobman. University of Michigan Press, Ann Arbor. 35 cents. 10 x 6½; 38; 1941 (paper).

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOOLOGY. *Vol. 43, No. 14. Studies of Some Amoebae from a Termite of the Genus Cubitermes,* by Joseph C. Henderson.

University of California Press, Berkeley. 25 cents. 10¼ x 6¾; 13 + 3 plates; 1941 (paper).

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOOLOGY.

Vol. 45, No. 1. Devescovinid Flagellates of Termites. I. The Genus Devescovina, by Harold Kirby.

University of California Press, Berkeley. $1.25. 10¼ x 6¾; 71 + 9 plates; 1941 (paper).

INDEX CATALOGUE OF MEDICAL AND VETERINARY ZOOLOGY. *Part 5. Authors: E to FYNNEY. U. S. Department of Agriculture.*

By Albert Hassall, Mildred A. Doss, Ruth M. Taylor, Gertrude B. Carson, and Dorothy B. Segal. Government Printing Office, Washington. 45 cents. 9⅛ x 5¾; 1177–1458; 1941 (paper).

BOTANY

FLOWERS AND FLOWERING PLANTS. *An Introduction to the Nature and Work of Flowers and the Classification of Flowering Plants. Second Edition.*

By Raymond J. Pool. McGraw-Hill Book Co., New York and London. $3.50. 9 x 5¾; xxiii + 428; 1941.

The merited success of the first edition of this excellent text over the past twelve years has resulted in the issue of a second edition.

The basic principle on which the entire book rests is the recognition of the plant as a living, working mechanism. The work deals almost entirely with the taxonomic aspect of botany, and in line with this, emphasizes the family as the important unit in classification. The formula method in depicting the prominent floral features of the various families in the master chart (to which the key constantly refers) is known as the Besseyan system, and was originated by the author's former professor, the late Charles Edwin Bessey. While the main features of the present edition follow closely those of the earlier work, the present does include several notable changes. An entirely new chapter on the vegetative characteristics of flowering plants has been added, and changes throughout the text have been made to include the recent work in plant taxonomy.

The text and key are well supplied with charts and illustrative material, both graphic and photographic. Several concluding chapters deal with the history of plant taxonomy, and the collecting, preserving, and mounting of herbarium specimens. A final chapter of reference books, monographs, manuals, and floras, a glossary, and an index conclude the volume.

THE REDWOODS OF COAST AND SIERRA. *Second Edition (Revised).*

By James Clifford Shirley. University of California Press, Berkeley. $1.25. 9½ x 6½; 84; 1940 (board).

The first edition of this work appeared in 1937 (cf. Q. R. B., Vol. 12, p. 115). The revision does not markedly differ from the earlier version. It suffers from a peculiar diffuseness of style, so that there is a good deal of repetition. Also, since the first edition appeared, the claim of the Sequoias to be the oldest living things has been seriously challenged twice by organisms of much humbler appearance—the cycads of New Zealand and certain single-celled plants obtained from the interior of rocks of geological age. Both of these seem to be entitled to the same serious consideration that the author gives to certain other long-lived plants that are not especially closely related to the redwoods. Also, the claim to have the greatest diameter of any tree in the world has been made on behalf of the chestnut "Tree of One Hundred Horses" near Catania, which is associated with Napoleon Bonaparte. And in 1909 the *National Geographic Magazine* published a photograph of a *Eucalyptus* with a diameter of 67 feet, and another still larger. Exaggerated statements as to the height of Australian eucalyptus trees may be safely discounted, but it is difficult to explain away a photograph. The reader of the work now under discussion is likely to be disappointed by the absence of any reference to these trees.

Of course, in a book as brief as this one it is obviously impossible to include enough material to satisfy all readers. The author has assembled a great deal of information not readily available elsewhere, and his product is worthy of all the praise bestowed upon it in these columns when the first edition appeared.

TEXTBOOK OF BACTERIOLOGY. *Thirteenth Edition, Revised.*

By Edwin O. Jordan and William Burrows. W. B. Saunders Company, Philadelphia and London. $6.00. 9⅛ x 5⅛; xii + 731; 1941.

The success of the earlier editions of this standard textbook have established its worth in the scientific field. The present volume is, with minor exceptions completely rewritten and is constructed upon a somewhat different basis than its predecessors. The most obvious manifestation of this change is the elimination of chapters devoted to the highly specialized applied fields, such as soil, industrial and dairy bacteriology, and the incorporation of parts of these, together with other old and much new material, in a lengthy chapter on bacterial physiology. The relation of bacteria to disease is also considered in its broad aspects. The subject of immunity has been completely reorganized and is considered in two chapters, the first of which discusses antigens and related material, while the second is devoted to specific resistance to infectious disease. Some of the new material in this edition includes sections on dental caries, the non-sporulating

anaerobic bacilli, the pleuropneumonia-like organisms, the Rickettsiae, and graphical representation of the secular prevalence and seasonal incidence of the more important infectious diseases. The illustrations are well chosen and extremely well reproduced. The book has been carefully and extensively documented and a total of over 1400 references are given as footnotes throughout the volume. A complete index concludes this excellent college and medical school text.

MODERN FRUIT PRODUCTION.

By Joseph Harvey Gourley and Freeman Smith Howlett. The Macmillan Company, New York. $4.50. 9¼ x 6⅛; vii + 579; 1941.

Since orcharding and fruit culture are assuming ever greater importance in American agriculture, it is not strange to find an increase in the number of good texts dealing with the technique and economic importance of fruit growing.

After an introductory chapter on the economic aspects of the fruit industry, the present text leads into a discussion of the fundamentals of physiology, morphology, soils, and chemistry as related to fruit plants and their ability to yield products of fine quantity and quality. Such broad topics as orchard sites and soils, the planning and setting of orchards, fertilizers and manures, pruning and propagation, harvesting, storing and marketing of fruits are discussed in considerable detail, yet free from the technical language which usually limits the use of good texts to the professional man only. An extremely fascinating and informative chapter on the origin and improvement of fruits has been included.

Each chapter lists the literature cited in that chapter, and the volume is concluded by a 12-page detailed index. The work will be of exceptional value in the hands of students of horticulture as well as orchardists.

PRINCIPLES OF MICROBIOLOGY.

By Francis E. Colien and Ethel J. Odegard. The C. V. Mosby Company, St. Louis. $3.00. 8½ x 5½; 444; 1941.

This fine text fully justifies its boast of presenting something new in the field of microbiology. After a preliminary discussion of the history, the important men, materials, and techniques of bacteriology, the important pathogenes are discussed from the point of view of what they do, rather than what they are. Emphasis throughout the volume is placed on the importance of bacteriology in nursing and disease prevention, rather than as a subject for specialization. In consequence, the work will find wider use in the hands of student nurses, medical students, and public health workers, than in those of the specialized bacteriologist.

The text is well supplied with tables, charts, and photographic illustrations (both monochrome and dichrome). A short list of references is appended to each chapter. A catalogue of the methods of preparing the various culture media, a suggested laboratory program including 21 units of work, a glossary, and a complete index conclude the volume. The excellence of the text is still further enhanced by the use of the new eye-tone paper.

THE PLANT WORLD. *A Text in College Botany.*

By Harry J. Fuller. Henry Holt and Company, New York. $3.25. 8½ x 5¼; xi + 592; 1941.

The author has prepared this college text primarily for use by students who are registered in elementary botany courses but who do not intend to continue with advanced work. The author believes that the primary objective of such a course, designed for cultural and general educational purposes should be the presentation of the fundamental features of the structure, physiological activities, and reproduction of flowering plants. The textual material is divided into four main parts: the nature of plants and of plant study; the structure and physiology of flowering plants; a general discussion of the plant kingdom, including a very interesting and instructive presentation of plant diseases; and, finally, the distribution of plants in time and space. A summary is placed at the end of each chapter. The excellent illustrations and colored plates are a distinguishing characteristic of the volume. The appendix contains a modern classification of the plant kingdom, a complete glossary, and an index.

PRUNING TREES AND SHRUBS.

By Ephraim P. Felt. Orange Judd Publishing Co., New York. $2.00. 7¾ x 5; 237; 1941.

Felt, Director and Chief Entomologist of the Bartlett Tree Research Laboratories, presents in this book the conclusions of years of research and practical experience in the art of pruning trees and shrubs. Working in conformity to the laws of nature, trees and shrubs are adapted by pruning in such a way as to best serve the diverse human needs of present-day living. In clear, non-technical language the author gives the principles of pruning not only shade trees, but fruit trees, nut trees, flowering shrubs and hedges, woody vines, and small fruits, as well. Ninety-three illustrations serve to clarify the text. All through the book the importance of training the tree while young in the way it should grow, is stressed.

A REVISION OF MELANCONIS, PSEUDOVALSA, PROSTHECIUM, AND TITANIA. *University of Michigan Studies: Scientific Series. Volume XIV.*

By Lewis E. Wehmeyer. University of Michigan Press, Ann Arbor. $2.50. 9¼ x 6; viii + 161; 1941.

This is a taxonomic study of the genera of fungi given in the above title. For the specialist only.

CONTRIBUTIONS DE L'INSTITUT BOTANIQUE DE L'UNIVERSITÉ DE MONTRÉAL, *No. 32.* Contains the following articles: *Sur deux formes nouvelles de Micrasterias, by Jules Brunel; Les prothalles de Lycopodes dans le Québec, by Roger Gauthier and Rolland Dumais; Notes floristiques sur l'est de la Nouvelle-Écosse, by Jacques Rousseau.*

Institut Botanique de l'Université de Montréal, Montréal. 25 cents. 9 x 6; 62; 1938 (paper).

BIBLIOGRAPHIE DES TRAVAUX BOTANIQUES *Contenus dans les "Mémoires et Comptes rendus de la Société Royale du Canada", de 1882 à 1936 inclusivement. Contributions de l'Institut Botanique de l'Université de Montréal, No. 33.*

By Jacques Rousseau, Marcelle Gauvreau, and Claire Morin. Institut Botanique de l'Université de Montréal. 50 cents. 9 x 6; 117; 1939 (paper).

LA FLORULE DE LA GROSSE-ILE. *Contributions de l'Institut Botanique de l'Université de Montréal, No. 34.*

By Frère Marie-Victorin and René Meilleur. Institut Botanique de l'Université de Montréal, Montréal. 25 cents. 9 x 6; 20; 1940 (paper).

HISTOIRE DE LA NOMENCLATURE DE L'ACER SACCHAROPHORUM K. KOCH (A. SACCHARUM MARSHALL) DEPUIS 1753. *Contributions de l'Institut Botanique de l'Université de Montréal, No. 35.*

By Jacques Rousseau. Institut Botanique de l'Université de Montréal, Montréal. 50 cents. 9 x 6; 66; 1940 (paper).

NOUVELLES ENTITÉS DE LA FLORE PHANÉROGAMIQUE DU CANADA ORIENTAL. *Contributions de l'Institut Botanique de l'Université de Montréal, No. 36.*

By Frère Marie-Victorin and Jacques Rousseau. Institut Botanique de l'Université de Montréal, Montréal. 50 cents. 9 x 6; 74; 1940 (paper).

MORPHOLOGY

OPTICAL ACTIVITY AND LIVING MATTER.

By G. F. Gause. Biodynamica, Normandy, Missouri. $2.75. 9½ x 6½; 162; 1941.

This work is a discussion of asymmetry and dyssymmetry. By definition the first of these terms is made to apply to the arrangement of molecules in a structure, and the other to the arrangement of atoms in a molecule. Such structures can not be superimposed on their mirror images, to which they bear a heterostrophic relation. The author's thesis is that in inert substances either form of a heterostrophic pair can occur about as often as the other, but that in living organisms one form will always displace the other. This is reminiscent of a doctrine promulgated sometime ago, that if two species occupy the same niche in the environment one of them will disappear. The theory seems borne out by the author's own experiments, but his bibliography of 21 pages covering over a century of investigation makes no mention of the pioneer work of Gulick on the Achatinellidae which have a different story to tell. Also, it contains only one item from the publications of Boycott, Diver, and their satellites on inverse symmetry.

The work is stimulating, but much more experimentation is needed before the theory can meet with universal acceptance.

FUNDAMENTALS OF COMPARATIVE EMBRYOLOGY OF THE VERTEBRATES.

By Alfred F. Huettner. The Macmillian Company, New York. $4.50. 9¼ x 6; xiv + 416; 1941.

It is obvious that the present volume is the product of long years of teaching experience. The clearness and order of the exposition are evidence of it. But, in addition, the author has for the major part provided original illustrations that actually reproduce the objects seen and do not require, as is often the case, a tremendous effort of cerebration and a vivid imagination. The subject matter is contained in 19 chapters of which the first four are devoted to an introduction to the subject, history of embryology, cell structure, and reproduction. A fifth chapter deals briefly with amphioxus. Chapters 6 to 8 describe the embryology of the frog, and chapters 9 to 15 that of the chick. These descriptions are accurate, detailed, and expressed with remarkable simplicity of style and language. The final chapters deal with mammals and man. There is an index but no list of references. Except for this omission, the present textbook satisfies the most exacting requirements. It will undoubtedly prove very popular for college courses.

CYTOLOGY, GENETICS, AND EVOLUTION. *University of Pennsylvania Bicentennial Conference.*

By M. Demerec, Charles W. Metz, Franz Schrader, Albert F. Blakeslee, Th. Dobzhansky, Clarence E. McClung, Herbert S. Jennings, William F. Diller, T. M. Sonneborn, Leon Churney, William R. Duryee, Paul S. Henshaw. University of Pennsylvania

Press, Philadelphia. $2.00. 9 x 6; v + 168; 1941.

This is a collection of papers by twelve of the most eminent biologists of the country. The topics covered concern a variety of approaches, techniques, and problems but all referring to the elements of the cell, their properties, and behavior. Space is not available to review the papers in detail but it is to be remarked that few symposia have produced such an aggregate of stimulating articles as we have here. One does not find the dull reexamination of well-known past accomplishments nor the repetition of textbook statements. The investigators represented are probing deeper into the fundamentals of biology and the student can find no more illuminating record of the advances being made or hoped for than the summary presented in this volume.

HUMAN ANATOMY AND PHYSIOLOGY.

By Nellie D. Millard and Barry G. King. W. B. Saunders Company, Philadelphia. $3.00. 7⅞ x 5¼; vii + 525; 1941.

This book has been prepared for the use of nurses and certainly seems to be satisfactory for the purpose. Of course, it is elementary and this is particularly noticeable with reference to the style in which it is written. The exposition of the subject matter follows a rather novel style which deserves to be remarked. A functional approach has been employed. The description of each organ or organ-system is introduced by a discussion of its general functions, then the morphology, and finally the physiology of the structure is dealt with. Thus, the skeletal muscles are described as muscles which move "apart", for example, the femur, and they are arranged in opposing groups; flexors and extensors, adductors and abductors, instead of the usual grouping of muscles of the thigh. Many of the illustrations are original and commendable.

THE PLAGIOSTOME HYPOPHYSIS, *General Morphology and Types of Structure.*

By Harry W. Norris. Obtainable from the Author, Grinnell, Iowa. 50 cents (paper); $1.00 (cloth). 10 x 6¾; 91; 1941.

The hypophysis of the plagiostome fishes (herein to include all elasmobranch fishes except the Holocephali) has been investigated in this anatomical study. On the basis of 51 genera the writer concludes that the plagiostome hypophysis has no exact detailed homologue in other vertebrates. The lobes of the plagiostome hypophysis, however varied in size, shape, and situation, or in attachments and other relations to brain, saccus vasculosus, and cranial walls, always conform to the definite plagiostome hypophysial type. The anterior and interior lobes vary but little from species to species, but the ventral is highly variable in many ways.

CYTOLOGICAL OBSERVATIONS ON ENDAMOEBA BLATTAE. *Illinois Biological Monographs, Volume XVII, Number 4.*

By Paul A. Meglitsch. The University of Illinois Press, Urbana. $1.00. 10⅜ x 6¾; 147; 1940 (paper).

In this study on *Endamoebe blattae*

a comparison of the results proceeding from the use of basic dyes and the Feulgen reaction were made in order to determine the relationship of basophilic material to nucleic acids, as demonstrated by the Feulgen reaction, throughout the life cycle up to the formation of the mature cyst, . . . As a result of the study, in addition to details of nuclear division during the trophic and cystic stages, it has been possible to observe a cyclical variation in the quantity and distribution of nucleic acid, as determined by the Feulgen test, correlated with the processes of nuclear division and encystment. Several unusual relationships between the basophilic material and the nucleic acid-containing material have also been observed.

Eight fine plates (91 figures) and a bibliography conclude this careful study.

THE PRINCIPAL NERVOUS PATHWAYS: *Neurological Charts and Schemas with Explanatory Notes. Second Edition.*

By Andrew Theodore Rasmussen. The Macmillan Company, New York. $2.50. 11 x 8⅜; ix + 73; 1941.

In this second edition of very useful charts of the principal pathways of the nervous system the author has included well-established alterations which investigative work in the field since 1932, the year of the first edition, has contributed. No basic changes in organization of the material or in the form of the charts have been made. The book should continue to prove helpful particularly to medical students.

PHYSIOLOGY AND PATHOLOGY

NATIVE AFRICAN MEDICINE *with Special Reference to its Practice in the Mano Tribe of Liberia.*

By George Way Harley. Harvard University Press, Cambridge, Massachusetts. $3.00. 9½ x 6; xvi + 294; 1941.

The author of this work was for many years a medical missionary in Liberia. The training which he received at the Kennedy School gave him an appreciative attitude toward native culture, and a desire to study the

medical practices of the natives from the standpoint of the student of folk-lore, as well as from that of the physician. The present volume is largely the result of his own observations among the medicine men of the Mano tribe, but it also contains a great deal of information about native medical practices throughout Africa, which he acquired from the leading libraries of London during a year of sick leave. While in London he and his wife studied botany, and after returning to Liberia they assembled a herbarium of over 1000 species, of which more than 100 have definite therapeutic value.

The ability of the medicine men to recognize different kinds of diseases is remarkable, and although they know nothing of the functions of the organs in the human body, in a particular case they can generally locate with uncanny accuracy the organ that is ailing. Each illness has its own method of treatment, in which internal medicine, external applications, massage, exercise, and magical incantation play their part. The latter may be the result of superstition but more often it is for the purpose of distracting the attention of onlookers, so that the real treatment and specific medicine may remain the secret of the medicine man. That some of the drugs used are really efficacious the author does not doubt; he cites authentic instances of successful treatment by native witch doctors of cases which the white physicians had abandoned as hopeless.

The knowledge of the correct treatment of specific diseases seems to have been acquired originally by the trial and error method, but today it is learned by joining one of the two great secret societies of Liberia—the Poro for men and the Sande for women. The initiation into these societies is laborious, painful, and expensive. Having paid the price for entry the "zo" cannot afford to let the general public in on his means of gaining a livelihood. To retain the respect and confidence of his clientele, elaborate ritual and even fraud are employed. The author describes treatments, some of them successful, which nevertheless were largely ceremonial. To draw the line between legitimate medicine and ceremonial magic is impossible. The two must be studied together. The ceremonial never injures the patient and the medicine may help, but the use of the blacksmith's tongs to restore a dislocated jaw bone seems slightly drastic.

An appendix lists over 200 plants believed by the natives to be medically useful. In transliterating the native names the author has had recourse to letters and diacritical marks that do not occur in the English alphabet, and the reader who finds himself confronted by these strange symbols is likely to regret that there is no explanation of their meaning given. Such would improve the book, as would also a few more photographs similar to the lonely frontispiece. There is an index of 16 pages and a bibliography of 7 pages.

SCHOOL HEALTH SERVICES. *A Study of the Programs Developed by the Health Department in Six Tennessee Counties.*

By Frank Walker and Carolina R. Randolph. The Commonwealth Fund, New York. $1.50. 9 x 5¾; xi + 172 + 35 tables; 1941.

For years school children all over the country have been receiving physical examinations of one sort or other, but only in a few places have any attempts been made to set up the organization for corrective work. In view of the findings of the selective service examinations the question arises as to the value of school health programs. This monograph provides a bit of information on the point. In Tennessee it is required that school children be examined every two years and apparently in some instances provision has also been made for corrective work—although what the actual arrangements are is not clear from this report. The authors have examined the records of six selected counties to evaluate the effects of the program from 1930 to 1936. The main findings appear to be that twelve-year-old children in 1936 have less decayed teeth and diseased tonsils and better nutrition than the twelve-year-old children seen in 1930. Thus, it is assumed that some benefits have been obtained by the school health program even though with respect to visual defects no change in prevalence is noted. It is particularly significant to learn that only about 33 per cent of dental defects, about 4 per cent of throat defects, and 12 per cent of visual defects are corrected after any examination, and that repeated examinations do not apparently increase the frequency of correction. Unfortunately, the data on which the report is based are defective in many respects and, therefore, the value of the findings is considerably limited.

VERHANDLUNGEN DER DEUTSCHEN GESELLSCHAFT FÜR KREISLAUFFORSCHUNG. *XIII. Tagung zu Wiesbaden vom 6. Mai 1940. Hauptthema: Kreislauf und Atmung.*

Edited by Eb. Koch. Theodor Steinkopff, Dresden and Leipzig. RM. 10 (in Germany); RM. 7.50 (outside of Germany). 9¼ x 5¾; xxxii + 182; 1940 (paper).

References, contributions, and speeches of the German Society for Circulatory Research are embodied in this volume. The opening pages give a statement of the purpose of the association, the proceedings of the previous meeting, and the opening report to the group. In all, there are twenty-two papers presented, with the principal discussions which followed each report. The first gives a general review of studies on circulation and respiration, not as isolated works, but in an effort to combine the various aspects of the two functions into a unified whole. The second paper emphasizes

the clinical applications of studies on circulation and respiration, especially lung collapse therapy. The chemical control of the mutual interrelation between breathing and circulation is then discussed. Some of the more important of the remaining papers concern the clinical aspects of silicosis in its effects on cardiac insufficiency, the effect of anoxemia produced by high altitude flying or experimental low oxygen concentration, lung ventilation and circulatory insufficiency in conjunction with certain related pathological conditions, experimental studies on circulatory collapse due to heart infarction, investigation of peripheral circulation by means of ultra red light, and electrocardiographic studies among twins. Most of the papers contain very good photographs, diagrams, and bibliographies. The volume itself is concluded with an index of authors and subjects.

BLUTDRUCKMESSUNG UND KREISLAUF IN DEN ARTERIEN DES MENSCHEN. *Geschichte und heutige Lage der Probleme neue Lösungsversuche.*

By Henrich von Recklinghausen. Theodor Steinkopff, Dresden und Leipzig. RM. 30.00 (outside Germany). 9⅛ x 6¼; xx + 532; 1940 (paper).

The early pages of this volume discuss the historical development of methods used for the measurement and recording of blood pressure and pulse curves. Diagrams of the various types of apparatus are given and results of the observations are critically discussed. Particular attention is paid to the findings upon which the step-curves are built up. Two principal types are described in detail, the pulse amplitude step-curve and the pulse form step-curve. The author next takes up the mathematical and graphic analysis of the pulse wave and the dynamics of arterial circulation, describing at some length the alterations which occur in the various components of the wave as it progresses to different points along the arteries. The significance of these findings for the practical determination of blood pressures by direct and indirect methods, and also the application to certain clinical conditions is thoroughly treated. A fourteen-page summary covers the general information in the text, but proper understanding of such details as the systolic and diastolic criteria can be obtained only by reference to the text itself. Several tables at the end of the volume outline the criteria used by various observers, summarize the mathematical formulae, and show in brief the principal hemodynamic principles. There is an adequate bibliography and a good index.

FAMILY FOOD CONSUMPTION AND DIETARY LEVELS. *Five Regions. U. S. Department of Agriculture, Miscellaneous Publication No. 405. Consumer Purchases Study. Farm Series.*

By Hazel K. Stiebeling, Day Monroe, Callie M. Coons, Esther F. Phipard, and Faith Clark. Government Printing Office, Washington. 35 cents. 9⅛ x 5¾; vi + 393; 1941 (paper).

FAMILY EXPENDITURES FOR HOUSING AND HOUSEHOLD OPERATION. *Five regions. U. S. Department of Agriculture, Miscellaneous Publication No. 432. Consumer Purchases Study. Urban and Village Series.*

By Hazel Kirk, Day Monroe, Kathryn Cronister, and Margaret Perry. Government Printing Office, Washington. 25 cents. 9⅛ x 5¾; v + 244; 1941 (paper).

The first of these publications presents information on the food of farm families at different income levels in the 66 counties surveyed. The relationships between income and family composition, consumption of different types of food, and nutritive value of farm family diets are some of the topics discussed.

The second publication, dealing with expenditures for housing and household operation of families living in villages and small cities, but excluding relief groups, foreign-born, one-person and broken families, and Negroes, except in the Southeast where they were studied as a separate population group, gives interesting comparisons between the patterns of the spending of home owners and of renters. Both volumes include the statistical data on which the studies were based.

FATAL PARTNERS: *War and Disease.*

By Ralph H. Major. Doubleday, Doran and Company, New York. $3.50. 9 x 6; ix + 342; 1941.

The course of history has often been profoundly changed by disease even more than by the outcome of wars. Some of the mightiest armies have fallen before typhoid, typhus, or bubonic plague, and have been scourged by scurvy. For the many centuries during which the sword and spear were the chief weapons and seige the established method of warfare, these diseases were the principal enemies of soldier and civilian alike. Later, progress in medical science largely eliminated the danger of such epidemics, and still more recent advances have almost banished malaria and yellow fever from the causes of fatalities. However, other grave medical problems have arisen consequent upon the use of explosives and mechanization of armies. Major tells a fascinating story of the companions in destruction, disease and war, from the days of the ancient Greeks to the present struggle. No war has been without some advance in medical knowledge, since wars serve as vast laboratories for testing discoveries made during times of peace. Although we still read of typhus in some of the armies of the present conflict, and of trench fever in air raid shelters, the principal problems concern shell shock and treatment of

infections. These, too, are yielding to advances in the study of psychiatry, to rapid ambulance service, and to chemical treatment. "The present war illustrates, more than any other war in the history of the world, that the science of saving life, as well as the science of destroying life, has made great progress."

PAPERS OF WADE HAMPTON FROST, M.D. *A Contribution to Epidemiological Method.*

Edited by Kenneth F. Maxcy. The Commonwealth Fund, New York. $3.00. 9¼ x 6; viii + 628; 1941.

Wade Hampton Frost was a fine teacher and his precepts have had a tremendous influence on the development of epidemiology in this country. His efforts were never directed towards the elaboration of theories, but, being what might be called a naturalist of crowd diseases, he stressed always the need for accurate observations, simple and logical quantitative analysis, and above all, clear thinking. These attributes are in evidence in all of Frost's writings and particularly in the 20 papers which Maxcy has brought together and briefly discusses. The articles are grouped into five sections. The first two include reports on field investigations in which Frost himself participated at the beginning of his career. The third section includes the papers resulting from the studies on influenza and the common cold. The final two sections contain articles dealing in the main with the methodology of epidemiology. In a sense these are the most interesting inasmuch as they reveal Frost's broad conception of public health problems, an outlook which has not yet been fully appreciated by the profession. A complete bibliography of Frost's writings is appended, and Maxcy has also contributed a short biographical note.

AN INTRODUCTION TO MEDICAL SCIENCE. *Second Edition, Thoroughly Revised.*

By William Boyd. Lea and Febiger, Philadelphia. $3.50. 9¼ x 5⅝; 358; 1941.

Nurses and premedical students often find difficulty in combining their studies of anatomy, bacteriology, physiology, histology, and genetics into an integrated whole. These are often presented as apparently separate subjects, and each is highly complex in itself. This volume (for earlier edition, cf. Q.R.B., Vol. 12, p. 380) demonstrates how the several studies must be considered together for attainment of an adequate understanding of medical problems. The first part deals with the general principles of circulation, inflammation, bacterial infections, parasitism, and natural resistance. The second, and major portion of the book, concerns the pathology of specific diseases presented, by and large, according to organ systems. The closing chapters consider practical application, preventive medicine, and the value of the nurse to the laboratory.

Although the treatment of each section is necessarily brief, it is thoroughly understandable. The small photographs are good, but the drawings are mostly inferior. The volume is well written, fulfills its purpose, and is adequately indexed.

IMMUNITY AGAINST ANIMAL PARASITES.

By James T. Culbertson. Columbia University Press, New York. $3.50. 9 x 6; viii + 274; 1941.

Both the beginning and the more experienced student of immunity to the parasitic forms should welcome this very considerable contribution in a field of investigation not overly burdened with clear and concise published works. Essentially, researches of devious and diverse nature form the material basis of this book. Its value is further enhanced by the predominance of fact everywhere—personal concepts and theories being practically eliminated. The textual material is presented in three parts: (I) Natural resistance and acquired immunity, in which natural and age resistance, requisites for immune response, parasites which elicit immunity, and mechanisms and demonstration of immunity are discussed; (II) Immunity in specific diseases, including the amoebiases, leishmaniases, trypanosomiases, malarias, coccidioses, trematodiases, cestodiases, nematodiases, and response to arthropods; (III) Applied immunity, describing the classification of and vaccination against parasites, and the diagnosis of parasitic infection. Ably and coherently written, carefully and extensively documented with over 1300 references, completely indexed, and attractively printed, the volume will prove very useful to the beginner, the trained investigator, and the practicing physician and veterinarian alike.

FUNDAMENTALS OF HEALTH: *Its Development and Conservation. Revised Edition.*

By T. Bruce Kirkpatrick and Alfred F. Huettner with the Collaboration of Clara Mae Taylor. Ginn and Company, Boston. $3.50. 8¼ x 5⅜; ix + 595; 1941.

The material included in the original edition of this text was based upon a systematic survey of the interests and requirements of university students. It was found that the students wanted and needed a knowledge of bodily structure, function, and development as a foundation upon which to build proper health habits and attitudes, and not a mere recitation of hygienic dogmas. After observing the reactions of several thousand students during the past eight years, the writers feel that their original convictions were sound. The present edition incorporates the more recent findings concerning embry-

ology, nutrition, internal secretions, bacteriology, immunology, and public health. As in the original writing, there is a considerable amount of space devoted to the principles of evolution, heredity, development, the function of the various organ systems, and proper health procedures for the maintenance of proper function. The photographs and diagrams are of only average quality, but there is an excellent list of selected readings. The volume contains a glossary and is well indexed.

INFANTILE PARALYSIS. *A Symposium Delivered at Vanderbilt University, April, 1941.*
By the National Foundation for Infantile Paralysis. National Foundation for Infantile Paralysis, Inc., New York. $1.25. 9 x 6; v + 239; 1941.

This book contains much informative material for physicians and health officers. The six lectures, by well-known specialists, approach the problem from as many different angles and embody all the recent knowledge concerning this disease. It is now recognized that there may be as many strains of poliomyelitis virus as types of pneumococci and that the disease differs in different species of susceptible animals. With the discovery of the virus in feces and sewage, a new lead has been given as to the way in which poliomyelitis is spread. The problem seems to be growing in complexity but it is by no means insoluble, as this survey indicates. In addition to the sections on the history, etiology, immunology and serology, pathology and pathogenesis, and epidemiology of poliomyelitis, there is a chapter on treatment and rehabilitation of the patient which will be extremely useful to physicians and nurses. A bibliography of 575 titles and an index are provided.

THE PARASITES OF MAN IN TEMPERATE CLIMATES.
By Thomas W. M. Cameron. The University of Toronto Press, Toronto. $3.00. 9 x 5⅞; xi + 182; 1940.

This work is based on a course of animal parasitology given in the medical school of McGill University. It is intended for the medical man who practises in the English-speaking temperate and sub-tropical zones. Only parasites which actually occur in North America or Great Britain are discussed in detail; those which may be introduced in patients from the tropics, but which cannot become acclimatized, are dealt with as briefly as possible, while odd, aberrant, or doubtful forms are omitted entirely. Since the volume is not designed for the student of tropical medicine or for the parasitologist or laboratory worker, the material has been selected to include only that required by the practitioner. The chapters deal with protozoa, helminths, leeches, and arthropods, with a final chapter on parasitological technique. The bibliography has been reduced to a minimum and only monographic or similar works have been included. The book is enriched by appropriate illustrations and is indexed.

PERSONAL HYGIENE APPLIED. *Seventh Edition, Revised.*
By Jesse Feiring Williams. W. B. Saunders Company, Philadelphia. $2.50. 7⅓ x 5¼; xvi + 529; 1941.

A college textbook of proven leadership in its field. However, there is no reason why this book should be limited to school or college, since physicians, teachers, nurses, and social workers may safely recommend it to parents or patients in need of guidance for living. Some of the new material in this edition includes an up-to-date consideration of the vitamins, a simplified discussion of infection and immunity, a rewritten chapter on the endocrines, a revised consideration of the safety problem as it relates to the automobile, and a new discussion of human heredity and its effects on the abilities and talents of the individual. The illustrations are especially praiseworthy. Questions and exercises and a list of selected readings are placed at the end of each chapter. The appendix provides a suggested list of topics for a term report, and a typical "true-false" test as given at Columbia University. A comprehensive index concludes this excellent textbook.

THE BODY FUNCTIONS: *Physiology.*
By Ralph W. Gerard. John Wiley and Sons, New York. Chapman and Hall, London. $1.75. 8⅓ x 5⅜; xiii + 289; 1941.

This book is one of a series (Wendt Science Series) designed to give the reader more than just a superficial survey of the sciences, but at the same time to avoid the burden of technical terms. Part one concerns the effectors and regulators of the body—muscles, nerves, internal secretions—and how they function. The second section deals with circulation, respiration, digestion, excretion, protective mechanisms, and reproduction. The central nervous system and behavior are discussed in the closing chapter. Enough anatomy, histology, and biochemistry are presented throughout the pages to clarify the descriptions of functions, and numerous simple physiological experiments are described, assuring a thorough understanding of the principles involved. Each chapter is concluded with an excellent list of references, and the book contains a complete glossary-index.

THE FURTHERANCE OF MEDICAL RESEARCH.

By Alan Gregg. Yale University Press, New Haven, Oxford University Press, London. $2.00. 8 x 5⅜; ix + 129; 1941.

The Director for the Medical Sciences of the Rockefeller Foundation first attempts to define medical research, second to discuss the relations of institutions conducting or furthering medical research with each other—especially the relations between foundations and universities—and third, to give an insight into the qualifications and personality of the individual research worker. It is evident that the author is aware of the points of view of both the donor foundations and the recipient institutions. He gives a provocative discussion of the shortcomings of the present system of foundation organization and the distribution of grants for research purposes in the United States, together with suggestions for improvement. The book is based on the eighteenth series of Terry Lectures delivered at Yale University.

THE COMPLETE WEIGHT REDUCER.

By C. J. Gerling. With a Foreword by Winfield Scott Pugh. Harvest House, New York. $3.00. 8 x 5½; 246; 1941.

This is in the nature of a handbook for the corpulent individual. In it will be found, under headings arranged alphabetically, brief and easily comprehended discussions of types of food, popular diet systems, reducing menus, commercial products, reducing machines, forms of exercise—in fact, very nearly everything that quackery as well as sound investigation has produced for the guidance of those who find themselves with overweighted constitutions. Numerous frauds are exposed. The book is intended only for persons who have no chronic functional or organic disorder, and only for those adults, who, having a moderate degree of overweight, wish to reduce in a rational manner. There is no index to the volume but this is unnecessary with the arrangement of the material in dictionary form.

X-RAY THERAPY OF CHRONIC ARTHRITIS. (*Including the X-ray Diagnosis of the Disease*). *Preliminary Report Based on 100 Patients Treated at Quincy, Illinois.*

By Karl Goldhamer. With a Foreword by Harold Swanberg. Radiologic Review Publishing Co., Quincy, Illinois. $2.00. 9 x 5¾; 131; 1941.

The chapter headings of this discussion on the x-ray diagnosis and treatment of chronic arthritis are as follows: Clinical aspects and pathology of chronic arthritis; Roentgen findings in chronic arthritis; How do x-rays act in chronic arthritis?; What cases should be treated by x-rays?; Technique of treatment; Report of patients; Results; Conclusions. The author found that "The results of irradiation were good in almost all forms of chronic arthritis and were startling and decisive in some types." A list of 52 references is given but there is no index.

BIOCHEMISTRY

ANNUAL REVIEW OF BIOCHEMISTRY. *Volume X.*

Edited by James M. Luck and James H. C. Smith. Annual Reviews, Inc., Stanford University P.O., Cal. $5.00. 8¾ x 6; xi + 692; 1941.

The editors call to the reader's attention a serious impact of the war upon the *Review*, namely, the irregularity and delay in the receipt of many journals. "Almost every article in the present volume has been submitted by its author with apologies for the restrictions in content imposed by the unavailability of recent numbers of important journals." Another effect is upon the international character of the *Review*. It is expected, however, that in Volume XI, the international character will be more manifest than in Volume X.

Twenty-four papers make up the volume. All of them are important for the biochemist, but the general biologist will also find a number that are of especial interest to him. The chapter on bioluminescence should not be missed. Others are on plant growth substances, spectrometric studies in relation to biology, mineral nutrition of plants, relation of soil and plant deficiencies and of toxic constituents in soils to animal nutrition. The two longest reviews are on hormones (52 pages) and water-soluble vitamins (48 pages). As is the custom, all papers are documented and the volume concludes with author and subject indexes. In the autumn of 1941 a cumulative author and subject index to Volumes I to X was published. Those possessing a full set of this valuable series are indeed fortunate.

OUT OF THE TEST TUBE. *Third Edition Revised and Expanded.*

By Harry M. Holmes. Emerson Books, Inc., New York. $3.00. 9 x 6; 305; 1941.

To the average intelligent layman, the field of chemistry represents one of the most appealing and revealing of all the subjects under investigation by modern scientific man. The present volume (cf. Q. R. B., Vol. 12, p. 495 for earlier edition) makes a very real and very definite contribution to the chemical education of the general reader. This excellent popularization represents the efforts of an expert in writing a simple, straightforward, and up-to-date account of the marvels of chemistry and the effect of these on our everyday lives. A few of the more interesting of the forty-odd chapters are concerned with: the importance of high vacua; hydrogen—the lightest substance known; oxygen—the elixir of life;

chemical warfare; atom smashing; silks and cellulose; fuels and smoke; chemistry and the motor car; chemistry of foods and nutrition; chaining the sun; the chemist in crime detection; the farm as a factory; what transportation owes to the chemist; minerals and world power; and the house of the future. The concluding chapter on strategic raw material is especially timely. The book is indexed and contains over one hundred striking illustrations. It is heartily recommended to all those who have an acute and healthy interest in the life of modern man and who wish to keep abreast of the contributions of chemical science to the comfort and convenience of living in the twentieth century.

POLAROGRAPHY. *Polarographic Analysis and Voltammetry. Amperometric Titrations.*

By I. M. Kolthoff and J. J. Lingane. Interscience Publishers, New York. $6.00. 9 x 5¾; xvi + 510; 1941.

A presentation of a thorough and critical assay of the theory, then of the practice, of the polarographic analytical method so far developed. The delicacy, extreme range, and the automatic nature of the method available make it of great value for all analysts—inorganic, organic, or biological. To be used, polarographic analysis must be well understood. The present volume goes far in its effort to explain the "ins and outs." Following this explanatory part, detailed methods of analysis are presented for many elements—complex salts, organic radicals and compounds, cancer tissues, etc. An important part of the text is the critical review of the literature through December, 1940. The appendix, which contains a table of potentials of common reference electrodes, and one of half-wave potentials of inorganic substances, and a chart of half-wave potentials of common inorganic substances in various supporting electrolytes, can be purchased separately. Author and subject indexes conclude the volume.

PLANT GROWTH SUBSTANCES. *Their Chemistry and Applications, with Special Reference to Synthetics. Second Edition, Revised.*

By Hugh Nicol. Chemical Publishing Company, Brooklyn, N. Y. $2.00. 8½ x 5½; xii + 148; 1941.

The first edition of this book was devoted almost entirely to the chemistry of substances, mainly synthetic, that produce, control, or regulate the growth of plants. Some physiological aspects are included in the present edition. When the book was first published the principal application of synthetic substances had related almost entirely to the treatment of cuttings. Recent work in the treatment of seeds and in grafting has now been included. Although the vitamins B (thiamin) and C (ascorbic acid) have been discovered to be potent growth regulating substances when applied to plants, there is little discussion concerning these except by indication of the most important studies. Rather, more attention is devoted to the less publicized indole and naphthyl compounds. Author and subject indices are provided.

DIE METHODEN DER FERMENTFORSCHUNG. *Lieferung 8.*

Edited by Eugen Bamman and Karl Myrbäck. Georg Thieme Verlag, Leipzig. R. M. 34.50 (outside of Germany). 11 x 8; 2589–3047; 1941 (paper).

This is the last volume, with the exception of the bibliography which will appear separately, of the important series on biological compounds, and techniques and methods applicable to enzyme investigation. In it are described the distribution, purification, properties, and actions of aspartase, peroxydase, katalase, hydrogenase, catalytic systems of unknown actions such as RSSR—RSH, ascorbic acid, and quinonoids. CO_2 assimilation by green plants and certain bacteria, N_2 assimilation, antienzymes and various models of enzyme action are also discussed. The latter part of the volume deals with enzymes important to industry and to the clinic (in particular, those apparently specific in carcinomas), the trends of future work along these lines, and the productive fields which enzyme research is opening up.

AN INTRODUCTION TO ORGANIC CHEMISTRY. *Fourth Edition.*

By Roger J. Williams. D. Van Nostrand Company. $4.00. 8½ x 5⅝; xiii + 628; 1941.

With justifiable pride the author points (in his preface) to the characteristics which have made this textbook so popular that it has gone through four editions and nine reprintings since 1927. Among the main features of the book is its logical exposition with emphasis on the relationship between organic and inorganic chemistry. For example, the ethers, esters, acyl halides, etc. are conceived and described as belonging to a group of acidic anhydrides with fundamental properties in common. In this revision the necessary additions consequent to recent discoveries have been made, but on the whole the contents and style of exposition are the same as those of the previous editions. There can be no doubt that the book will retain its high position as a college textbook.

SEX

CLINICAL AND EXPERIMENTAL INVESTIGATIONS ON THE GENITAL FUNCTIONS AND THEIR HORMONAL REGULATION.

By Bernhard Zondek. The Williams & Wilkins Co., Baltimore. $4.50. 9 x 5¾; xxiv + 264; 1941.

In this volume are brought together a series of reports on the author's work in Palestine since 1935. The investigations have covered a wide field but the results are all of interest to the general biologist as well as to the endocrinologist. There is a report on the occurrence of some extrogenic substances in nature—in the waters of the Dead Sea, among other places. The problems studied may be classed under two general groups. The first deals with the effects of the administration of extrogenic and androgenic hormones. Experiments and observations are reported with reference to the percutaneous application of the hormones—the morphological and physiological changes produced by the duration of the administration of the substances in varied dosages. The second group of studies contains the findings related to the menstrual cycle and its mechanism. The author outlines his hypothesis on the mechanism of menstruation which in his view is produced "by harmonious action of the gonadotropic and ovarian hormones independently of the ovum." Much of the work summarized here is already known but the value of this volume is not diminished thereby, particularly since the author has attempted to integrate his own and the findings of others. One must remark and admire the experimental technique which, although sometimes open to criticism, reveals nevertheless the ingenuity and cleverness associated with Zondek's name. A bibliography of 269 titles and a summary of the work on the subject prior to 1935 are included.

BIOMETRY

STATISTICAL ACTIVITIES OF THE AMERICAN NATIONS. 1940. *A compendium of the statistical services and activities in 22 nations of the Western Hemisphere, together with information concerning statistical personnel in these Nations.*

Edited by Elizabeth Phelps. Inter American Statistical Institute, Washington, D. C. $2.00. 9⅛ x 6; xxxi + 842; 1941.

This volume, prepared under the direction of the Temporary Organizing Committee of the Inter American Statistical Institute, has for its aim "to present a current account of the *statistical services and activities* of the American nations, together with a partial biographical list of the principal *statistical personnel* in those nations other than the United States." It is the outgrowth of the realization for some years past of the need to bring into closer relation the statisticians of the various American countries and to make them acquainted with the fact-gathering activities of these different countries and the publications that are the outgrowth of such activities. Each one of the 22 American republics is represented in a series of descriptive papers. These are summarized both in the language of the country and in English. The articles cover such topics as the system of official statistics, including a discussion of censuses and a list of the principal government agencies which compile statistics; principal official serial statistical publications; statistical educational facilities; statistical library facilities; statistical societies or associations; and principal non-official or semi-official statistical agencies and their serial publications. One of the important features of the volume is the Biographical Directory of Statistical Personnel which covers 58 pages. Three appendixes contain general information on Statistical sources, Notes on the statistical section of the Eighth American Scientific Congress, and the Inter American Statistical Institute. An excellent index completes the volume.

STATISTICAL ATLAS OF SOUTHERN COUNTIES. *Listing and Analysis of Socio-Economic Indices of 1104 Southern Counties.*

By Charles S. Johnson and Associates: Lewis W. Jones, Buford H. Junker, Eli S. Marks and Preston Valien; Consultants: Edwin R. Embree and W. Lloyd Warner. University of North Carolina Press, Chapel Hill. $4.00. 10 x 7; x + 355; 1941.

The sociological features of thirteen Southern states, by counties, are analyzed in this atlas. A great number of these features concern the educational characteristics of the areas, showing by race the expenditures per student percentage attendance, type and value of the schools, and per cent of illiteracy. The remaining features concern economic characteristics, including types of occupations, ownership and tenancy, order of major crops, and per capita wealth. From an analysis of these characteristics the counties have been classified into cultural types. It was found that geographical propinquity does not necessarily result in similar county types. This and other observations are briefly discussed, most of which have long been known but have not been adequately expressed quantitatively. Though doubtful, it is to be hoped that the toil and expense of preparing this volume will be warranted. The information might prove of value to leaders in rural educational programs because of the close interrelationship between the school and the socio-economic conditions of the surrounding area. The bibliography contains approximately 600 references.

THE SECOND YEARBOOK OF RESEARCH AND STATISTICAL METHODOLOGY. *Books and Reviews.*

Edited by Oscar Krisen Buros. The Gryphon Press, Highland Park, New Jersey. $5.00: Less ten per cent on orders sent directly to The Gryphon Press. 10½ x 7½; xx + 381; 1941.

The second volume of this compilation is considerably enlarged. It contains reviews of 359 books published in English since 1933, of which 125 appeared in the first volume (noted in Q. R. B., Vol. 14, p. 378). The reviews have been culled from 283 journals. Unquestionably a useful source of information, this yearbook is also entertaining, and sometimes embarrassing for book reviewers. The editor would like to make the *Yearbook* an annual publication if funds could be obtained; otherwise it will remain biennial. Other and more ambitious changes are contemplated, including the review of articles as well as of books. The value of this proposal is doubtful.

THE BULLETIN OF MATHEMATICAL BIOPHYSICS. *Volume 4, Number 1, March, 1942.*

Edited by N. Rashevsky. University of Chicago Press, Chicago.

This number contains the following papers: Diffusion as a Function of Aggregates in Colloidal Media, by Herman Branson; A Theory of Steady-State Activity in Nerve-Fiber Networks: IV. N Circuits with a Common Synapse, by Alston S. Householder; A Kinetic Theory of Diffusion Forces in Metabolizing Systems, by H. D. Landahl; Suggestions for a Mathematical Biophysics of Auditory Perception with Special Reference to the Theory of Aesthetic Ratings of Combinations of Musical Tones, by N. Rashevsky; Non-Linear Excitation Theory: Non-Accommodative, Sub-Threshold Effects, by Alvin M. Weinberg.

PSYCHOLOGY AND BEHAVIOR

TERRITORIAL AND MATING BEHAVIOR OF THE HOUSE WREN. *Illinois Biological Monographs, Volume XVIII, Number 3.*

By S. Charles Kendeigh. The University of Illinois Press, Urbana. $1.50. 10½ x 7; 120; 1941 (paper).

This exhaustive and valuable study of the house wren is the result of 19 years of observation of 142 male and 147 female wrens on a 15-acre estate. The results make it obvious that an intensive directive study reveals many facts otherwise not ascertained in casual field observation.

Adult males that have previously nested almost invariably return to the same territory that they formerly occupied, or they establish a new territory adjacent to it. The return of adult females to their former nesting areas is almost as regular. The female does not defend territory or recognize the limits of territory as established by the male. When the female appears confined to a territory, it is due to her nest-box being centrally located within the territory, to her being chased out of neighboring territories, or to the male's adjustment of the outlines of his territory to coincide with her movements.

Territorial boundaries are frequently in a state of flux and rarely remain uniform throughout the season. These changes are caused by early arriving males attempting to take possession of very large territories, parts of which they are forced later to yield, to the impact of new males arriving and carving out territories, to variations in the activity and feeding areas of the female mate, to the shifting population of both males and females between the first and second breeding periods, and the necessity for remating. Territory is maintained throughout each breeding period and breeding season, although there may be some decrease in activity as nesting progresses. The non-breeding population of males varies from 28 to 35 per cent of the total male population and in the females from 13 to 20 per cent of the total female population. Except for the fact that only the male sings, sex recognition is based on differences in behavior of the two sexes. Later, there may be recognition of each other as individuals through characteristic mannerisms. Remating of a pair the following year occurred in 42 per cent of the cases where both birds of the pair survived and returned to the locality.

Besides the conclusions derived from the writer's observations, case histories of territories of individual males compiled during the course of this work are given "in order to make available to others the vast amount of information that accumulated at the Baldwin Bird Research Laboratory from 1914 to 1939."

DEVELOPMENTAL DIAGNOSIS: *Normal and Abnormal Child Development. Clinical Methods and Practical Applications.*

By Arnold Gesell and Catherine S. Amatruda. Paul B. Hoeber, Inc., New York. $6.50. 9⅛ x 6½; xiii + 447; 1941.

A series of publications on the pioneer work of Gesell and his co-workers has preceded this book. *Developmental Diagnosis*, which is destined to become a classic, has the advantage over these earlier books in that it is much more inclusive as regards subject matter. It also gives the most concise and workable presentation to date of the Gesell clinical testing material. In the preface Gesell states that:

Observations of normal behavior threw light on maldevelopment; and the deviations of development in turn helped to expose what lay beneath a deceptive layer

of "obviousness" in normal infancy. We have come to sense the identity of the developmental processes which in equal measure determine the reaction patterns of the intact and the defective child, the well endowed, the partially endowed, and those blemished by injury and disease.

It is these deep, determining developmental processes which must inevitably come within the scope of clinical medicine. In preparing this volume we have had much in mind the medical student who in private or public capacity will soon be confronted with varied and exacting problems which concern the developmental welfare both of normal and abnormal children.

From a study of the genesis and growth of patterns of behavior Gesell has been able to formulate concrete norms of maturity which have been given thorough practical tests and have proved dependable "not only in the study of normal variations of development, but in the diagnosis and supervision of pediatric, neurological and psychiatric conditions."

The emphasis throughout the book is on diagnosis. In the first section the basic principles and methods are first outlined and the nature of behavior and of mental growth discussed. Chapter III, by far the longest in the book, is the most basic in that it "integrates the developmental tests, the behavior characteristics, and the growth trends of the behavior patterns for the period from 4 weeks to 3 years. This chapter is organized for convenient reference and is illustrated with over a hundred photo-tracings of normative behavior patterns." Part II, dealing with defects and deviations of development, discusses problems of differential diagnosis, amentia and retardation, amentia of high grade, low grade amentia, endocrine disorders, convulsive disorders, the neurological diagnosis of infant behavior, cerebral injury, special sensory handicaps, prematurity, precocity, environmental retardation, and clinical aspects of child adoption. Part III is concerned with the protection of early child development—diagnosis and guidance and development supervision. Four appendices give details concerning technique, charts, equipment, and cinematic case studies. The volume is provided with an excellent working index.

BASIC PROBLEMS OF BEHAVIOR.

By Mandel Sherman. Longmans, Green and Company, New York, London and Toronto. $3.00. 8½ x 5⅝; vi + 440; 1941.

Many books concerned with personality and adjustment suffer from an excess of clinical evidence and a lack of scientific fact. This book, an elaboration of the author's *Mental Hygiene and Education* (1934), demonstrates that, in the investigation of problems of behavior, clinical and experimental evidence can be brought together with successful results. This alliance is accomplished by the selection of suitable experiments from the huge amount of psychological literature, and practical illustrations furnished from clinical data. The opening pages present a systematic discussion of emotion as a foundation for the following chapters on motivation and frustration (including experimental neurosis), personality, adjustment mechanisms, attitudes, conflicts, neurosis, and mental abnormalities. A valuable chapter on delinquent behavior discusses current theories of the psychogenic basis, personality, and treatment of this problem. Gathering together as much data as it does, this book should prove valuable for reference as well as for use as a text, and may well encourage a closer association between psychologist and psychiatrist, as the author suggests. One might wish a more critical treatment of personality tests and procedures used in measuring attitudes. A 16-page bibliography and index are included.

BREATHING CAPACITY AND GRIP STRENGTH OF PRESCHOOL CHILDREN. *University of Iowa Studies in Child Welfare, Volume XVIII, Number 2.*

By Eleanor Metheny. University of Iowa Press, Iowa City, Iowa. $1.35 (paper): $1.70 (cloth). 9¼ x 6½; 207; 1940.

This investigation is designed to study the possible relationship of breathing capacity and grip strength to health and physical condition. Until now data concerning this problem in preschool children have been scarce. Special spirometers and dynomometers were constructed suitable to the physical requirements and need for special motivation of the children. Complete information was obtained concerning anthropometric measurements, intelligence scores, health and fatigue ratings, sex, and age. In the analysis of data on approximately 200 children the intelligence quotient was found to be unrelated to either grip strength or breathing capacity but height was most highly correlated with both factors. It is doubtful that breathing capacity is related to health of preschool children, but on the average the children with higher physical condition ratings had greater grip strength. The material suggests that the latter variable may be related to the run-down condition preceding a cold. This careful study justifies further investigation of grip strength as a functional test for children.

A BEHAVIOR STUDY OF THE COMMON TERN (STERNA HIRUNDO HIRUNDO L.). *Proceedings of the Boston Society of Natural History, Vol. 42, No. 1.*

By Ralph S. Palmer. Society of Natural History, Boston, Mass. $1.00. 9 x 6; 119 + 14 plates; 1941 (paper).

A number of notable field studies and reports on the natural history of the common tern have appeared in recent literature, but none has dealt so fully with the

individual and social behavior of the bird as the present investigation. The author's careful field observations extending over several years in the terneries at the Sugarloaf Islands off Sagadahoc County, Maine, are herein set forth with an excellent measure of scientific exactness and clarity. The detailed behavior of the tern from the time of its arrival at the ternery, through the mating, brooding, and rearing seasons, makes up the greater portion of the report. Notes on the requirements for a successful tern colony (isolation, food, and cover), the economic importance of the bird, as well as a list of its predators are included. The report concludes with an extensive bibliography, several charts, and a number of plates depicting the habitual activities of the tern.

SCHIZOPHRENIA IN CHILDHOOD.

By Charles Bradley. The Macmillan Company, New York. $2.50. 8 x 5¼; vii + 152; 1941.

As indicated by the title, the subject matter of this book is concerned with the schizophrenic reaction as it is seen in children. In the first three chapters the author gives a brief but appropriate summary of the development of the present-day schizophrenic concept through the influences of Kraepelin, Bleuler and Meyer. The viewpoint from which the remainder of the book is written seems to emphasize the "disease entity" rather than the "reaction type" concept, and the value of the book as a contribution to the literature is correspondingly weakened. Indicative of the contents and organization of the material are the chapter headings: Incidence, Symptomatology, Course, Types, Etiology, Psychopathology, Laboratory Findings, Anatomical Pathology, Diagnosis. The author leans to a constitutional basis, with secondary, precipitating situation factors as causative agents. The treatment is descriptive rather than dynamic. There is a bibliography of 118 titles. Subject and author indices are included.

A NEW TEST FOR THE DETECTION OF COLORBLINDNESS.

By P. B. Wiltberger. College Book Company, Columbus, Ohio. $8.00. 9 x 6; 22; 1941.

Many people who are classified as colorblind by the usual tests are not truly colorblind but have varying degrees of weakness in color perception. The writer of this book objects to the use of such tests for this and other reasons. He recommends the use of color "chips," or rectangles, on which the subject fixes for a short period of time. Upon shifting the fixation point the normal person (or a person who is only color weak) sees the complimentary color after-image, whereas the totally colorblind person sees a white rectangle.

The book contains a brief description of the physiology of color perception, directions for administration of the test, and several pages of color "chips." For some purposes this method may be useful, but in general people who administer tests of color perception are interested in detecting color weak individuals as well as those who are totally colorblind.

SOCIAL CASE RECORDS FROM PSYCHIATRIC CLINICS *with Discussion Notes.*

By Charlotte Towle. The University of Chicago Press, Chicago. $3.00. 9 x 5¾; xii + 455; 1941.

This book has been written primarily for use in the author's classes in psychiatric social work at the University of Chicago. The organization of the material is, accordingly, for usefulness in study and discussion. In a nine-page introduction the author formulates in concise and lucid form the general conceptual background against which the present-day psychiatric social worker operates. The remainder of the book is devoted to a presentation, in detail, of psychiatric social worker contacts with nine separate cases. The presentation of each case is followed by discussion notes and a pertinent list of references. There is an index. This book is recommended as an authoritative and practical contribution to its field.

CHILD PSYCHOLOGY: *Child Development and Modern Education.*

Edited by Charles E. Skinner and Philip L. Harriman. With the Collaboration of Amy F. Arey, L. A. Averill, Lorin E. Bixler, E. A. Bond, J. W. Charles, and Others. The Macmillan Company, New York. $3.00. 8⅜ x 5½; xii + 522; 1941.

A symposium of the general subject of child psychology. Fourteen different contributors are included. The general plan is a presentation of the problems of child psychology and a description of the methods employed in the scientific study of children. Throughout, the normal child is regarded as an integrated, growing personality. The book is well set-up and organized and the material is lucidly presented. Lists of references follow each chapter. In an appendix a brief, comprehensive outline of each chapter of the book is given. There are subject and author indices.

MENTAL HYGIENE IN EDUCATION.

By Ernest W. Tiegs and Barney Katz. Ronald Press Company, New York. $2.75. 8 x 5½; xiv + 418; 1941.

A mental hygiene book for teachers, administrators, supervisors and students of psychology. The material is presented in three parts: Part I. The nature and

origin of personality difficulties; Part II. Improving personal and social adjustment; and Part III. The more serious personality difficulties. The scope of the material is broad and the aim of the authors commendable, but the treatment inevitably reflects the doctor of philosophy rather than the doctor of medicine, and is academically descriptive rather than dynamic. It is doubtful whether the book will prove a practical guide in handling the personality problems of school children. A list of references follows each chapter and there are author and subject indices.

VISION. *A Study of its Basis.*

By S. Howard Bartley. With an Historical Perspective by Edwin G. Boring. D. Van Nostrand Company, New York. $3.50. 8⅜ x 5½; xv + 350; 1941.

A handbook on the psychophysiology of vision. The author presents material selected from the psychology of vision for which present day neuro-physiology has something to offer, and discusses certain related visio-sensory phenomena for which physiology must provide an answer. Aspects of vision touched on are indicated by some of the chapter headings: Forms of brightness discrimination, Entoptic stray light, Repeated stimulation, Flicker, Perception of movement, Neural interaction, Contour, The electroretinogram, The optic-nerve discharge, The cortical response. References are appended to each chapter, and there are name and subject indices.

JUVENILE DELINQUENCY: *A Comparative Study of the Position in Liverpool and England and Wales.*

By J. H. Bagot. Jonathan Cape, London. 5s. 8⅜ x 5⅜; 93, 1941.

This book presents the first of a new series of studies of social problems issued from the Division of Statistics in the Social Science Department of the University of Liverpool. The study is designed to throw light on the question of why the trend of juvenile delinquency is beginning to soar again with the advent of the present war. The study consists of a comparison of the position in Liverpool, England and Wales, and is based on detailed analysis of records of juvenile delinquency. The conclusions and recommendations are summarized in one of the final chapters.

ANXIETY AND ITS TREATMENT *with Special Reference to Alcoholism.*

By John Yerbury Dent. John Murray, London. 3s. 6d. 7⅜ x 4⅞; 124; 1941.

This is a consideration of the problem of alcoholism viewed as a symptom of an underlying anxiety. However, the author writes from the viewpoint which is of doubtful helpfulness and accuracy, that anxiety is essentially a chemical and physical manifestation rather than a manifestation of personality malfunction. Alcoholism is regarded as a chemical disease. One chapter is devoted to vitamin B deficiency. In another the treatment of addiction by apomorphine is described.

PARS PRO TOTO. *Ein Beitrag zur Pathologie Menschlicher Affekte und Organfunktionen. Schriftenreihe zur Deutschen Medizinischen Wochenschrift, Herausgegeben von R. Siebeck and V. v. Weizsäcker, Heft 5.*

By Rudolf Bilz. Georg Thieme Verlag, Leipzig. RM. 9.75 (outside of Germany). 8⅛ x 5¼; 318; 1940 (paper).

The author offers in this treatise a biologically oriented contribution to the pathology of human emotions and organic functions (neuroses). The investigation will interest all students of the "mind-body" problem, particularly biologists, psychologists, and psychiatrists.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

NATURAL HISTORY AND THE AMERICAN MIND.

By William Martin Smallwood in Collaboration with Mabel Sarah Coon Smallwood. Columbia University Press, New York. $4.25. 9 x 6; xiii + 445; 1941.

This is a pioneering work. Within the past few years a number of biographical works dealing with the naturalists of America have appeared, but this is the first one to focus its emphasis exclusively on the effect of their lives and work on contemporary and subsequent thought The men and women whom the authors have selected for special attention are not by any means the greatest, but those whom they consider to be the most significant: those who occupy not the mountain passes but the cross roads on paths to knowledge. Therefore, the personnel discussed in a work of this sort is largely a matter of opinion, and the present reviewer feels that the omission of Robert Chambers, whose *Vestiges of Creation* prepared the way for Darwin is very definitely a defect. Certainly Chambers through his influence on Darwin has affected later scientific thought as much as, if not more than, that other pre-Darwinian evolutionist, Rafinesque, whose erratic figure appears and reappears throughout the pages of this book. And the treatment of Amos Eaton seems somewhat out of proportion when compared to, for instance, that accorded Agassiz.

Except for such instances, however, the selection of personnel is above criticism. There is practically no naturalist who lived in the United States prior to 1850 who is not mentioned in the pages of this work. Some-

times the notice seems inadequate. For example, Charles Alexandré Lesueur is mentioned because he made the drawings for Godman's *Natural History*, thus setting a new standard for scientific illustration. Nothing is said about his romantic career with the ill-fated expedition of La Perouse, of which he was the only member to escape the destruction which overtook it. Neither is anything said about Lesueur's systematic work on pelagic mollusca, and only the briefest possible mention is made of his part in the establishment of the intellectual capital of the United States at New Harmony.

Again, John Bartram receives a great deal of attention, which of course he merits, but nothing is said about his spectacular discovery of *Franklinia*. But of course, if the authors had attempted to please all their potential readers (whose name should be Legion) they would have produced a work the size of the Cambridge Natural History. The chapter dealing with the sixteenth and seventeenth century writers was an eye opener to this reviewer, as was also the story of Jane Cloden of the eighteenth century, who was the first woman to take up any kind of scientific activity.

Perhaps the most original, and hence the most important chapter, is that dealing with the manufacturers of scientific instruments. We all use microscopes, but what do we know about Spencer, Tolles, Gronow, and Zentmayer? How many who use Spencer instruments know that at the age of sixty Spencer lost his entire plant, stock, and records in a fire, and then proceeded to set the entire world an example of courage and heroism by starting over again from scratch, five years later winning a gold medal at the Paris exposition?

To the authors of this work America means only the Atlantic seaboard of the United States. This example of inverse synecdoche leads them to repeat the popular error that the Museum of the Library Association in Charleston, South Carolina, was the first to be established in America. As a matter of fact, the Natural History Museum established by Kino at Matapé, Sonora, antedated that at Charleston by more than a century. Also, the authors' contention that American culture originated on the Atlantic seaboard can hardly be maintained, for when Harvard was founded in 1638 there were at least four universities on the Pacific slopes of Latin America, one of which at Leon, Nicaragua, had been in operation since 1523.

A more adequate index and a chronological table would have added to the efficiency of the work, as would have better documentation. But despite these criticisms the book is truly monumental and deserves universal circulation.

THE ROAD OF A NATURALIST.
By Donald Culross Peattie. Houghton Mifflin Company, Boston. $3.00. 9 x 5½; ix + 315; 1941.

Not since the publication of *The Desert* and *The Mountains* has the present reviewer come across a more beautifully expressed appreciation of nature than this work by Peattie. Like Van Dyke, Peattie understands the truth of the statement of a late philosopher, that "There is more real beauty in what science has to tell us of the chemistry of a distant star, or of the life history of a protozoon, than in any cosmogony produced by the creative imagination of a pre-scientific age." Both Van Dyke and Peattie give free rein to creative imagination, but both confine their statements to what science can reveal to us about the natural countryside. Here the resemblance ceases. Van Dyke is an art critic, Peattie is an artist. Instead of the impersonal and objective attitude of Van Dyke, Peattie is personal and subjective, and identifies himself with the desert and the mountains that he loves. In his case the antithesis between man and nature does not exist. Like the child in one of Kipling's *Just So* stories, he fades away into the landscape, and becomes part of nature. The mantle that has fallen upon his shoulders is not that of Van Dyke, but that of William Bartram, that gentle soul of an earlier century, who was so distressed by the cumber and entanglement of a war torn world that he retired to the wilderness to commune with nature and nature's God.

Peattie is not inspired by the desert so much as by the feelings which it evokes within him. His poetic descriptions alternate with meditations of an intimate nature upon the deeper things of life, which will be found comforting by those who have endured the same sorrows, and there are many such, but they are not articulate and we seldom hear about them. The world has great need today of the mystic vision. It must be a great satisfaction to the author to know that he is helping to meet this need.

RESEARCH—A NATIONAL RESOURCE. *II.—Industrial Research. December, 1940. Report of the National Research Council to the National Resources Planning Board. National Research Council. Government Printing Office, Washington.* $1.00. 11¾ x 9; xi + 370; 1941 (paper).

Under the direction of the National Resources Planning Board three surveys have been made concerning research as a national resource, not only in relation to the present defense effort but also to developments in the post-defense period. The first of these reports, on "Relation to Federal Government of Research," has been published. The third, "Business Research," is in preparation. The second, the present volume, has been prepared by 26 outstanding leaders in research. From a summary of the findings we note the following:

Continuous and increasing application of science by industry is contributing most significantly to the high

standard of American living. Viewed in this light industrial research is a major national resource.... American industry employs over 70,000 research workers in over 2,200 laboratories at an estimated annual cost, based on an average of figures reported, of the order of $300,000,000.... Industrial research is possible for all industrial units, small and large.... Industry looks to the universities for trained technical men, and for principal advances on the frontiers of science.... There is opportunity for some American university to establish a comprehensive curriculum in applied mathematics. The number of men engaged in applied mathematics is comparatively small but their work is extremely significant.

Recommendations, in summary form, are also made to industry, to labor and industry, and to the Government for the further extension of research in industrial fields.

SCIENCE *versus* MATERIALISM.

By Reginald O. Kapp. Methuen and Company, London. 10s. 6d. 7¾ x 5¼; 280; 1940.

The author of this book is an engineer who seems, unfortunately, unfamiliar with the concept of *integration* in human biology. He attempts to answer, to his own satisfaction, the question "Is matter the only reality?" His revival of the battle between science and religion and materialism and vitalism would seem to be an earnest battle against windmills. The book is divided into three parts: I. Clearing the ground; II. Double determinateness; and III. The material universe.

By circuitous routes he clears his mind by resorting to the dichotomy of living and lifeless substance (i.e. organic vs. inorganic) and asserting that living substance is subject to a double set of restrictions, that its behavior is *more* determinate than that of lifeless substance. This "double determinateness" is regarded as evidence for vitalism. Likewise, living substance is constructed to a "specification," i.e. is not merely the result of shaking down, as in crystal formation and other inorganic aggregates. Many references are made to the views of various biologists, philosophers, and physicists, both ancient and modern.

It is felt that the puzzled reader will find little help in this exposition, and the causal reader little interest.

PHOTOGRAPHIC EMULSION TECHNIQUE.

By T. Thorne Baker. American Photographic Publishing Company, Boston. $4.00. 7⅞ x 5⅝; xii + 263; 1941.

"This book is intended not only to be a guide to practical emulsion making, but as a textbook for technical students, industrial chemists, and photographers generally, who are anxious for their own reasons to prepare emulsions of various types and speeds." Although the range of commercially produced sensitized paper, glass, and film is wide, the photographer occasionally requires an emulsion outside of this range and in such a small quantity as to make commercial production impossible. The writer thoroughly explains the technique of preparing emulsions, including selection of materials, laboratory layouts, coating, color, x-ray, ultraviolet, grain, speed, etc.

For deeply involved amateur photographers, study and experimentation with emulsions provides a fascinating hobby full of possibilities. For them this book may be recommended as an excellent guide. Yet a simple reading of these pages cannot but broaden the knowledge of those who depend entirely upon commercial products. Included are many references and a complete index.

SOIL AND SENSE.

By Michael Graham. Preface by Sir E. John Russell. Faber and Faber, London. 7s. 6d. 7¼ x 4¾; 274; 1941.

The fertility of the soil is to agriculture what petrol is to a motor car—it is what keeps it a going concern. In this simply written and very understandable volume, Graham has brought out the fact that increased mechanization, with its counterpart, decreased animal populations, has resulted in a serious strain on the fertility of the soil. This condition is further aggravated by the excessive and unwise use of cheap chemical fertilizers. In non-technical language, the author discusses the natural fertility cycle of the soil, as well as crop rotation, and the importance of grasses and legumes in maintaining soil fertility, and encourages the farmer to avail himself of the scientific tests now available to determine the needs of his soil, and to make up for the depletions with a good grade of chemical fertilizer. There is also a strong plea for landlords to assist tenants in supplying the needed fertilizer.

Since the book is about British agricultural problems there is little beyond the very broadest considerations which will be of value to the American farmer. A short list of references and an index are appended.

THE ROCKEFELLER FOUNDATION: *Annual Report for 1940.*

By Raymond Fosdick. The Rockefeller Foundation, New York. Free. 8½ x 5⅝; xv + 473; 1941 (paper).

In the first part of this report is given President Raymond B. Fosdick's review of the year's work of the Foundation. Then follow detailed reports for the different divisions: International Health, Medical, Natural and Social Sciences, Humanities, and Work in China. Appropriations for the year amounted to

$9,854,497. Of this sum, 77 per cent was for work in the United States and 23 per cent for work abroad. Public health received the largest share, followed by the natural, social and medical sciences, humanities, and rural reconstruction in China, in the order named. The war curtailed the work in some of the European countries but appropriations went to 44 countries in Europe, Asia, Africa, and the Americas. The activities of the Foundation, extending into all fields of intellectual endeavor, represent wise and careful planning on the part of those who have the responsibility of disbursing the funds. The largest single appropriation went to the University of California for the construction and housing of a giant cyclotron.

BY LIGHT OF SUN.

By Elsie Symington. With Foreword by Richardson Wright: Woodcuts by Claire Leighton. G. P. Putnam's Sons, New York. $2.00. 8 x 5½; x + 196; 1941.

Mrs. Symington's autobiography is the story of a sensitive woman's successful search for a way of living which would provide the widest scope for her physical and mental energies. Because the environment she sought turned out to be a special sort of house in a special sort of garden, the casual reader may be inclined to dismiss the work as just another garden book. It is a great deal more than that, for its author is a peculiarly articulate person, able to analyze and explain with great skill the various "drives" which warred within her and to make it understandable just why she finally chose to use all her force in the creation of a vast garden in which things are permitted to grow under the circumstances in which they grow best. In not many autobiographies is the author more precisely aware of her place in the scheme of things, her capacities and limitations. Women seem to have a talent for self-revelation and Mrs. Symington has cultivated her large share of that talent to make a book which has something in common with the great self-portraits of the past.

BIOLOGICAL STAINS: *A Handbook on the Nature and Uses of the Dyes Employed in the Biological Laboratory. Fourth Edition Revised.*

By H. J. Conn. With the collaboration of J. A. Ambler, R. W. French, W. C. Holmes, et al. Revised with the assistance of J. T. Scanlan, Anis P. Bradshaw, and Mary A. Darrow. Biotech Publications, Geneva, N. Y. $3.40. 8 x 5⅜; 308; 1940.

This recognized and authoritative handbook of dyes employed in the biological laboratory has been given a very careful revision and brought completely up-to-date. New material embodied includes description of thirteen dyes not previously considered. The subject covered so adequately by this book is becoming a field for more and more precise knowledge all the time and hence the urgent need for just such a volume as this. In addition to the succinct presentation of the nature and uses of the various dyes themselves, the book includes a discussion of the history and theory of staining, and the spectrophotometric analysis of dyes. The appendix contains much valuable information arranged in convenient tabular form. The volume is concluded with a complete bibliography and index. To students, technicians, and seasoned investigators everywhere, this manual of stain technology—one of the few acceptable to the discriminating scientist—should prove of inestimable and increasing value, as its previous editions have done.

AMERICA'S HOUSEKEEPING BOOK.

Compiled by New York Herald Tribune Home Institute. Charles Scribner's Sons, New York. $2.00. 8¼ x 5⅜; xxiv + 607; 1941.

A manual for the housewife. The book has been in the making for upwards of 15 years. It developed out of numerous letters and telephone calls from housewives for aid on household matters. Frequently, long and difficult research was necessary by the Institute staff to find solutions to some of these problems. The material is well organized under three headings: Home organization; Housekeeping methods; and Operation and maintenance of the home. The index, which covers 28 closely printed pages, gives some indication of the number of subjects covered. We mention only a few of these: electric shock, medicines, removing stains, heating systems, household pests, electrical repairs, paints and stains, repairing furniture, doors, etc., treatment of walls, and soaps. Many illustrations are included.

DIRECTORY OF MICROFILM SOURCES *including Photostat Service.*

Compiled by Rose C. Cibella. Special Libraries Association, New York. 75 cents. 10 x 7; vii + 56; 1941 (paper).

A directory for librarians, research workers, and industrialists. It has been issued to make available the data now in hand, but a revised edition is contemplated which will furnish a much more complete set of records. There are listed 202 universities and libraries which now provide microfilm or photostatic service, also a number of commercial firms. A group of sample order forms in use by various institutions, a geographical index of microfilm sources and an index to equipment help to make this directory extremely useful to those wishing to avail themselves of the fine opportunity offered by libraries in the United States, Canada, and England.